

A NEW ENALIARCTINE PINNIPED FROM THE ASTORIA FORMATION, OREGON, AND A CLASSIFICATION OF THE OTARIIDAE (MAMMALIA: CARNIVORA)

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ABSTRACT. The eastern North Pacific fossil pinniped genus *Enaliarctos* Mitchell and Tedford, 1973 (subfamily Enaliarctinae), includes the oldest and most primitive fossil species yet recognized in the family Otariidae. *Pteronarctos goedertae*, new genus and species, at nearly 19 m.y.a., is now the geologically youngest known species in the subfamily, is closely related to *Enaliarctos*, and is known only by one fossil skull from the basal part of a late Early Miocene to early Middle Miocene age sequence of strata referred to the Astoria Formation in coastal Oregon. *Enaliarctos mealsi* Mitchell and Tedford, 1973, and *E. mitchelli* Barnes, 1979, both known by skulls, are latest Oligocene to Early Miocene (circa 24–25 m.y.a.) in age and from the Jewett Sand in California. *Pteronarctos goedertae* has more derived characters than either species of *Enaliarctos* and also has some primitive characters. Because of this, neither species of *Enaliarctos* could have been ancestral to *P. goedertae*, and the group must have achieved diversity even prior to the Miocene. The third genus in the subfamily, *Pinnarctidion* Barnes, 1979, is more distantly related to *Enaliarctos* and *Pteronarctos* than those two genera are to one another.

Pteronarctos goedertae has a suite of characters also present in the later true sea lions and fur seals (subfamily Otariinae) and, more specifically, many of its characters either are present in, or could have been evolved into, the characters of the primitive fur seals of the fossil genus *Pithanotaria* Kellogg, 1925, and of the living genus *Arctocephalus* Geoffroy Saint-Hilaire and Cuvier, 1826. A revised classification of the family Otariidae, *sensu lato*, is presented to include *Pteronarctos goedertae* and other taxa described since the 1977 review by Repenning and Tedford. Taxonomic changes are proposed.

INTRODUCTION

Discoveries of important new fossils of sea lions, fur seals, walruses, and their diverse extinct relatives have precipitated

since about 1960 a series of research publications. This present paper is based on one such important new fossil, here named *Pteronarctos goedertae*, new genus and species, which was discovered in a coastal sea cliff in Oregon.

First, it is important to note that my use of the carnivore family Otariidae is in the broad sense (Mitchell, 1968, 1975; Barnes, 1972, 1979; also Barnes et al., 1985:table 1) and includes sea lions, fur seals, walruses, and their extinct relatives. This broadly drawn family is equivalent to the superfamily Otarioidea as used by Tedford (1976), Repenning (1976), Repenning and Tedford (1977), de Muizon (1978), and King (1983a).

The wholly extinct pinniped subfamily Enaliarctinae contains the earliest and most primitive known species in the Otariidae. When *Enaliarctos mealsi* Mitchell and Tedford, 1973, was described, the original authors interpreted it as being a very primitive otariid that had some similarities with the fur seals. Subsequent authors (Repenning and Tedford, 1977; Barnes, 1979) have been more specific in suggesting that it could actually have been ancestral to modern fur seals and sea lions of the subfamily Otariinae. I have described a geologically slightly younger, more derived, and somewhat aberrant Early Miocene species of *Enaliarctos* Mitchell and Tedford, 1973, *E. mitchelli* Barnes, 1979, which was contemporaneous with another, very different type of enaliarctine otariid, *Pinnarctidion bishopi* Barnes, 1979. All three of these species of enaliarctines were based on fossil skulls from the latest Oligocene to Early Miocene age Pyramid Hill Sand Member of the Jewett Sand in California's San Joaquin Valley. The oldest and most primitive known enaliarctine remains *Enaliarctos mealsi*. *Enaliarctos mitchelli*, which is from a stratigraphically higher level, has morphology that could have been derived from that of *E. mealsi*. *Pinnarctidion bishopi*, with a somewhat different suite of derived characters, could only have shared common ancestry with *Enaliarctos* prior to the Miocene. In the same paper (Barnes, 1979) I

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showed that the more derived subfamilies of Otariidae must have had even earlier origins than had been previously suggested.

The pinniped species that has generally been accepted as the earliest representative of the derived subfamily Otariinae (including extant fur seals, sea lions, etc.) is the Late Miocene fur seal-like animal *Pithanotaria starri* Kellogg, 1925 (see Repenning and Tedford, 1977), which is also known from California. The species has some derived characters that exclude it from consideration as a direct ancestor of later fur seals and sea lions, but it clearly is related to them and has a bearing on their origins (Repenning and Tedford, 1977; King, 1983a:132).

There has been a hiatus of nearly 14 million years in the known fossil record between this species and any named species of *Enaliarctos* (see Repenning and Tedford, 1977:fig. 6; Barnes, 1979:fig. 22; Barnes et al., 1985:fig. 6); however, this is the time during which the early Otariinae obviously must have evolved (Repenning and Tedford, 1977; King, 1983a:132).

Now, within late Early Miocene age rocks referred to the Astoria Formation on the coast of Oregon, a relatively late occurrence of a previously undescribed species of enaliarctine has been discovered, which helps fill the void in our information. While this animal shares many primitive features with the earliest Miocene species of *Enaliarctos*, it also has some derived characters that cause it to resemble the Recent fur seals of the genus *Arctocephalus* Geoffroy Saint-Hilaire and Cuvier, 1826, animals which are among the most primitive of the living Otariinae.

Only one other species of fossil pinniped, *Desmatophoca oregonensis* Condon, 1906, has been named previously from the same suite of rocks referred to as the Astoria Formation on the Oregon coast. *Desmatophoca oregonensis* is very distinct from enaliarctines, and it has been classified in a separate, more derived otariid subfamily, the Desmatophocinae (see Mitchell, 1968, 1975; Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Barnes, 1979, 1987). The type specimen of that species, the holotype of the baleen whale *Cophocetus oregonensis* Packard and Kellogg, 1934, and an important skull of *Desmostylus hesperus* were found farther north along the Oregon coast and higher stratigraphically in the same formation than the holotype of the new species of enaliarctine that is described here (Packard and Kellogg, 1934; Moore, 1963:89, pl. 3 [see geologic sections C and D]; Ray, 1976; Repenning and Tedford, 1977).

The purpose of the present paper is to describe the morphology and systematic position of the new enaliarctine from Oregon, to offer comments on the relationships of the fossil otariid species that have been described since Repenning and Tedford's (1977) review, and to propose a revised classification of otariid pinnipeds.

METHODS AND MATERIALS

The anatomical terminology used here is adapted from that of Howell (1928), Miller et al. (1964), Mitchell (1966, 1968), Hershkovitz

(1971), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). I have indicated which skull measurements in Table 1 are the same as those that were defined by Sivertsen (1954:18–20) by following them with the numbers given to them by Sivertsen. Other measurements are as defined by Barnes (1972:fig. 1, 1979:4–5). A complete synonymy of the subfamily Enaliarctinae is given here, and an emended diagnosis of the latter and a synonymy of the family Otariidae have been given by Barnes (1979). Ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979) following the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout (1981). Comprehensive reviews of the living species of Otariidae have been prepared by Scheffer (1958), King (1964, 1983a), and Ridgway and Harrison (1981). The latter reference is the authority I selected for systematics of Recent species. In cases where a family-group name is not used at the same rank and/or in the same context as originally proposed, the original author is shown in parentheses. Millions of years ago is abbreviated as m.y.a. The acronym LACM is for the Natural History Museum of Los Angeles County, Los Angeles, California; UCMP is for the University of California Museum of Paleontology, Berkeley, California.

The holotype skull is crushed by a few millimeters dorsoventrally, and the right side of the skull has been moved posteriorly relative to the left. The restorations (Figs. 2, 3b, 4b, 6) compensate for this. The matrix filling the external narial opening that is visible in Figure 1 was subsequently removed to show the structures visible in Figure 2. Anatomical abbreviations used in the illustrations are as follows:

ac—alisphenoid canal
Bo—basioccipital
Bs—basisphenoid
cc—carotid canal
eam—external acoustic meatus
fh—hypoglossal foramen
fi—incisive foramen
fio—infraorbital foramen
fl—lacrimal foramen
fla—anterior lacerate foramen
flp—posterior lacerate foramen
fo—foramen ovale
fop—optic foramen
fpal—palatine foramen
fpg—postglenoid foramen
Fr—frontal
fs—sphenopalatine foramen
fsm—stylomastoid foramen
g—glenoid fossa
hf—tympanohyal pit (= hyoid fossa)
Ju—jugal
mp—mastoid process
Mx—maxilla
Na—nasal
Oc—occipital
occ—occipital condyle
Pa—parietal
Pal—palatine
Pmx—premaxilla
Ps—presphenoid
Pt—pterygoid
pp—paroccipital process
Sq—squamosal
tb—tympanic bulla

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Infraorder Arctoidea Flower, 1869

Parvorder Ursida Tedford, 1976

Family Otariidae Gill, 1866

INCLUDED SUBFAMILIES. Enaliarctinae Mitchell and Tedford, 1973; Otariinae (Gill, 1866); Desmatophocinae (Hay, 1930); Allodesminae (Kellogg, 1931); Imagotariinae Mitchell, 1968; Dusingathinae Mitchell, 1968; Odobeninae (Allen, 1880).

Subfamily Enaliarctinae Mitchell and Tedford, 1973

Enaliarctinae Mitchell and Tedford, 1973:218; Mitchell, 1975: 19, fig. 1; Barnes, 1979:8; Barnes et al., 1985:table 1. "Common Ancestral Group." Repenning, 1975:29, fig. 11. Enaliarctidae. Tedford, 1976:367 (caption for fig. 2), 372 (table 1); Repenning, 1976:376; Repenning and Tedford, 1977:11; King, 1983a:fig. 3.1; *non* Takeyama and Ozawa, 1984:36; Dubrovo, 1981. Enaliarctidae. Árnason, 1977:241, typographical error.

TYPE GENUS. *Enaliarctos* Mitchell and Tedford, 1973.

INCLUDED GENERA. *Enaliarctos* Mitchell and Tedford, 1973; *Pteronarctos*, new genus; and *Pinnarctidion* Barnes, 1979.

Pteronarctos, new genus

DIAGNOSIS OF GENUS. A genus in the subfamily Enaliarctinae differing from *Pinnarctidion* by having skull with smaller antorbital processes, anterior openings of optic foramina located relatively higher within interorbital septum, no orbital vacuities in interorbital septum, palate narrower anteriorly and bearing one long palatine sulcus on each side extending anteriorly from largest posterior palatine foramen, smaller pterygoid process of maxilla ventral to orbit, cheek teeth relatively larger and more closely spaced, protocone shelf of P⁴ larger, anterolabial corner of M¹ large, palatines ventral to internal choana forming an elongate tube with rounded lateral edges, internal narial opening higher and narrower, strut formed by pterygoid spanning between palate and braincase thick and convex lateral to pterygoid hamulus, paroccipital process smaller and joined to mastoid process by thinner and narrower crest, and occipital condyles more prominent and separated ventrally by deeper intercondylar notch; differing from *Enaliarctos* by having skull with more nearly parallel cheek tooth rows, roots of P²-M¹ more closely appressed, P³ with bilobed posterior root, lesser carnassial function of P⁴ and M¹, as indicated by fusion of protocone root of P⁴ to posterolateral root and by shallower embrasure

pit for M¹ on palate between P⁴ and M¹, smaller M¹ with bilobed instead of trilobed root, larger and double-rooted M², larger supraorbital process of frontal, narrower posterior part of interorbital area, no pregenoid process on lateral part of glenoid process, more prominent anterolateral corner of braincase, shallower fossa on lateral side of braincase corresponding to pseudosylvian sulcus of brain, narrower squamosal fossa between braincase and zygomatic arch, incisive foramina (palatine fissures) entering external nares less vertically, smaller orbit, smaller external nares, and greater facial angle.

TYPE AND ONLY INCLUDED SPECIES. *Pteronarctos goedertae*, new species, late Early Miocene, Oregon.

ETYMOLOGY. Derived from Greek; *pteron*, for fin (also wing or feather), and *arktos*, for bear (also north); in reference to the pectoral flipper, which these primitive, aquatic, bear-like carnivores must have had. The root *Arctos* is commonly used in Otariid names.

Pteronarctos goedertae, new species

Figures 1-6, 7c

DIAGNOSIS OF SPECIES. As for the genus.

HOLOTYPE. LACM 123883, complete skull with right I³ and both upper canines, collected by Gail H. Goedert, 18 April 1981.

TYPE LOCALITY. LACM 5058, Jumpoff Joe, north end of Nye Beach, Newport, Lincoln County, Oregon.

FORMATION AND AGE. The holotype of *Pteronarctos goedertae* is late Early Miocene in age and is from the basal part of a rock unit referred to as the Astoria Formation. The name Astoria Formation was originally proposed for late Early Miocene rocks exposed at Astoria, Oregon, on the south side of the Columbia River, and the formation name has been subsequently applied to slightly younger rocks from late Early Miocene to early Middle Miocene age that were deposited in the Newport embayment along the coast of Oregon (Howe, 1926; Packard and Kellogg, 1934; Ray, 1976: fig. 2). The geologic section at the type locality of *P. goedertae* was described by Schenck (1928), Packard and Kellogg (1934: 4-7), and Moore (1963).

The holotype of *P. goedertae* was originally derived from a horizon just above the base of the Astoria Formation, where it contacts the underlying Nye Mudstone (Moore, 1963:94, pl. 33 [Section D]). The specimen was found in a block of a fine-grained gray, glauconitic sandstone whose original place in the sea cliff was determined by J.L. Goedert and G.H. Goedert. It came from a concretion-bearing horizon about five feet stratigraphically beneath the white, fine-grained tuffaceous shale that is shown by Moore (1963:pl. 33) in geologic Section D in the lower part of the Astoria Formation. The Astoria Formation and its contained molluscan fauna in this area were used by Addicott (1976:102, 104, fig. 4) to characterize the Newportian Molluscan Stage (see Armentrout, 1981). This stage, correlated with the early part of the "Temblor" provisional provincial mega-invertebrate stage, as characterized by Addicott (1972) on the basis of California fossils, and the Saucian foraminiferal stage (Addicott, 1976;



Figure 1. *Pteronartcos goedertae*, new genus and species, holotype skull, LACM 123883, from LACM locality 5058, dorsal view.

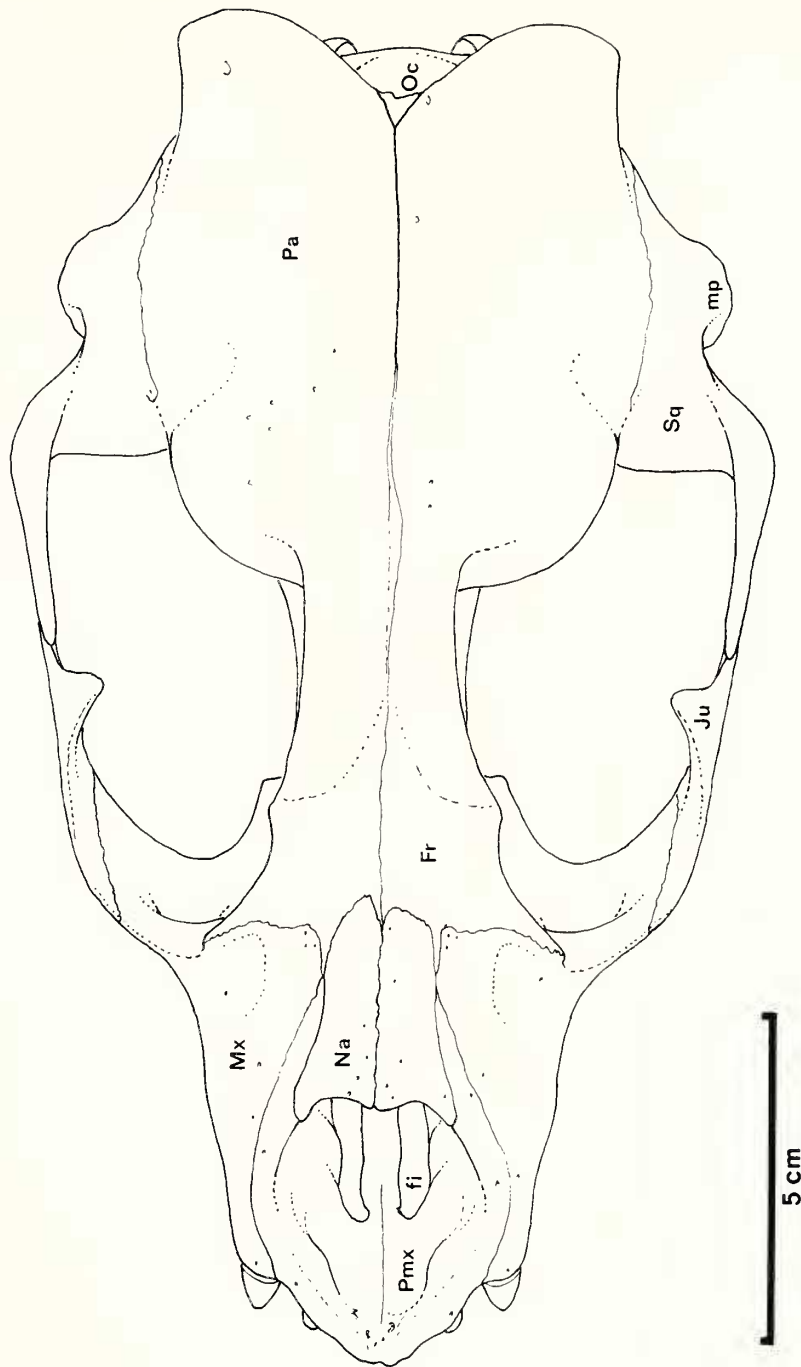


Figure 2. *Pteronarcos goedertae*, new genus and species, restoration of holotype skull, LACM 123883, dorsal view; for explanation of abbreviations see Methods and Materials.

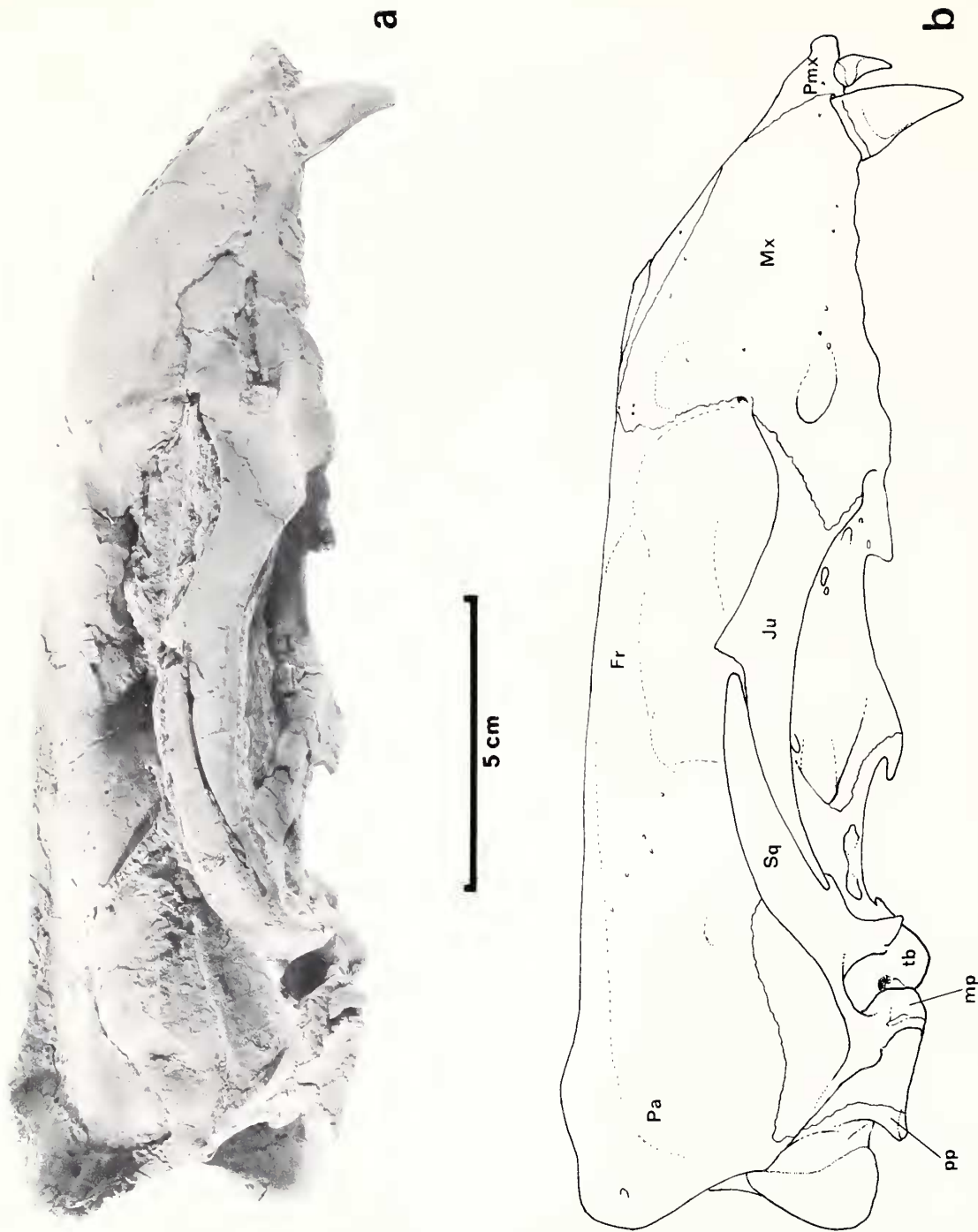


Figure 3. *Pteronarcos goedertae*, new genus and species, holotype skull, LACM 123883, from LACM locality 5058; **a**, right lateral view; **b**, restoration of right lateral view; for explanation of abbreviations see Methods and Materials.



Figure 4. *Pteronarcos goedertae*, new genus and species, holotype skull, LACM 123883, from LACM locality 5058; **a**, left lateral view; **b**, restoration of left lateral view with zygomatic arch omitted to show structures within the orbit; for explanation of abbreviations see Methods and Materials.

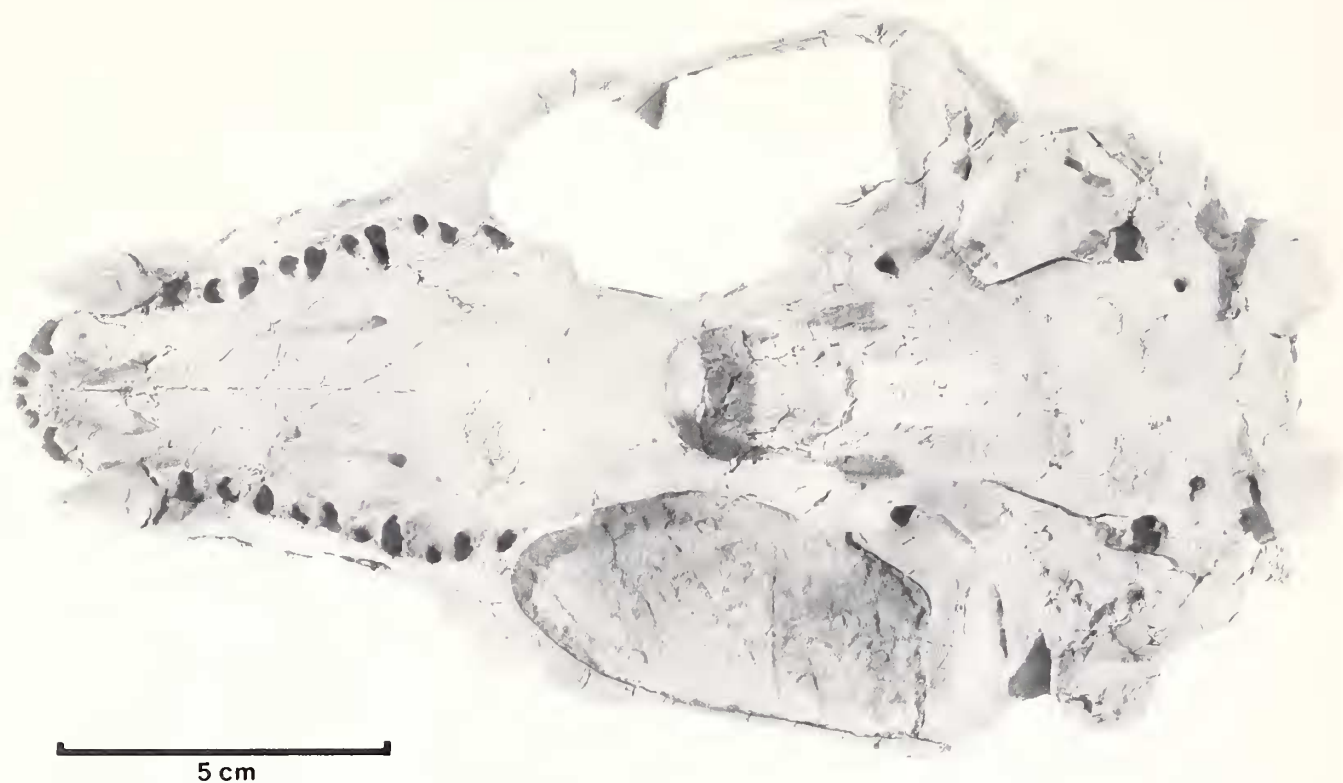


Figure 5. *Pteronarcos goedertae*, new genus and species, holotype skull, LACM 123883, from LACM locality 5058, ventral view.

and see Moore, 1963:20–21), has also been correlated with the Hemingfordian North American Land Mammal Age and the Burdigalian Stage of Europe, and this Oregon coastal section of the Astoria Formation therefore spans from approximately 15 to 19 m.y.a. (see Ray, 1976:fig. 2; Repenning and Tedford, 1977:table 1; Armentrout, 1981). Because the holotype of *P. goedertae* was found very close to the base of the stratotype of the Newportian Stage, its age is undoubtedly coincident with the old end of all of the above ages and it is probably close to 19 million years old.

Moore (1963:17) characterized the fossil mollusks in the Astoria Formation as indicating an environment of deposition in warm-temperate, true marine conditions in shallow to moderate depths over a substrate of silty mud to fine sand. These conditions are those under which the holotype of *P. goedertae* was fossilized and might have been part of its living environment.

ETYMOLOGY. The species is named in honor of Mrs. Gail H. Goedert of Gig Harbor, Washington, who collected the holotype. Mrs. Goedert and her husband, Mr. James L. Goedert, have made many important paleontological discoveries in the Pacific Northwest.

DESCRIPTION AND COMPARISONS. Skulls of *Enaliarctos mealsi* and *E. mitchelli* have been thoroughly described, illustrated, and compared (Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Barnes, 1979). Between the holotype (LACM 4321) and the referred specimen (LACM

[CIT] 5303) of *E. mealsi*, all but the anterior-most tip of the rostrum is known, and I have previously provided a revised cranial restoration of the species (Barnes, 1979). Only the front half of the skull of *E. mitchelli* is known. Fortunately, the holotype of *P. goedertae* is the most complete published skull of any species in the subfamily Enaliarctinae, and it provides considerable new information about these animals. It would be unnecessary, however, to duplicate here the description of cranial anatomy that is identical in *P. goedertae* and the previously described enaliarctines. Therefore, I describe the evidence from the holotype that bears on its individual sex, age, and depositional history, then some suites of characters whereby it differs from and resembles various other taxa, and offer some interpretations of these characters.

The holotype skull of *Pteronarcos goedertae* is nearly complete. The left mastoid and paroccipital processes were partially weathered away when the skull was exposed by wave action. The two canines remain in their alveoli, and the right I³ was found loose in matrix adjacent to the palate. All the other teeth have fallen out and are missing. As with many species of otariids, the cheek teeth have short roots, and upon death and decomposition of the animal, they readily fall out of the skull. The skull apparently underwent preburial transport but suffered little or no abrasion prior to fossilization. When laboratory preparation revealed all of the critical structures in the left orbit, it was decided not to remove the matrix filling the right orbit.

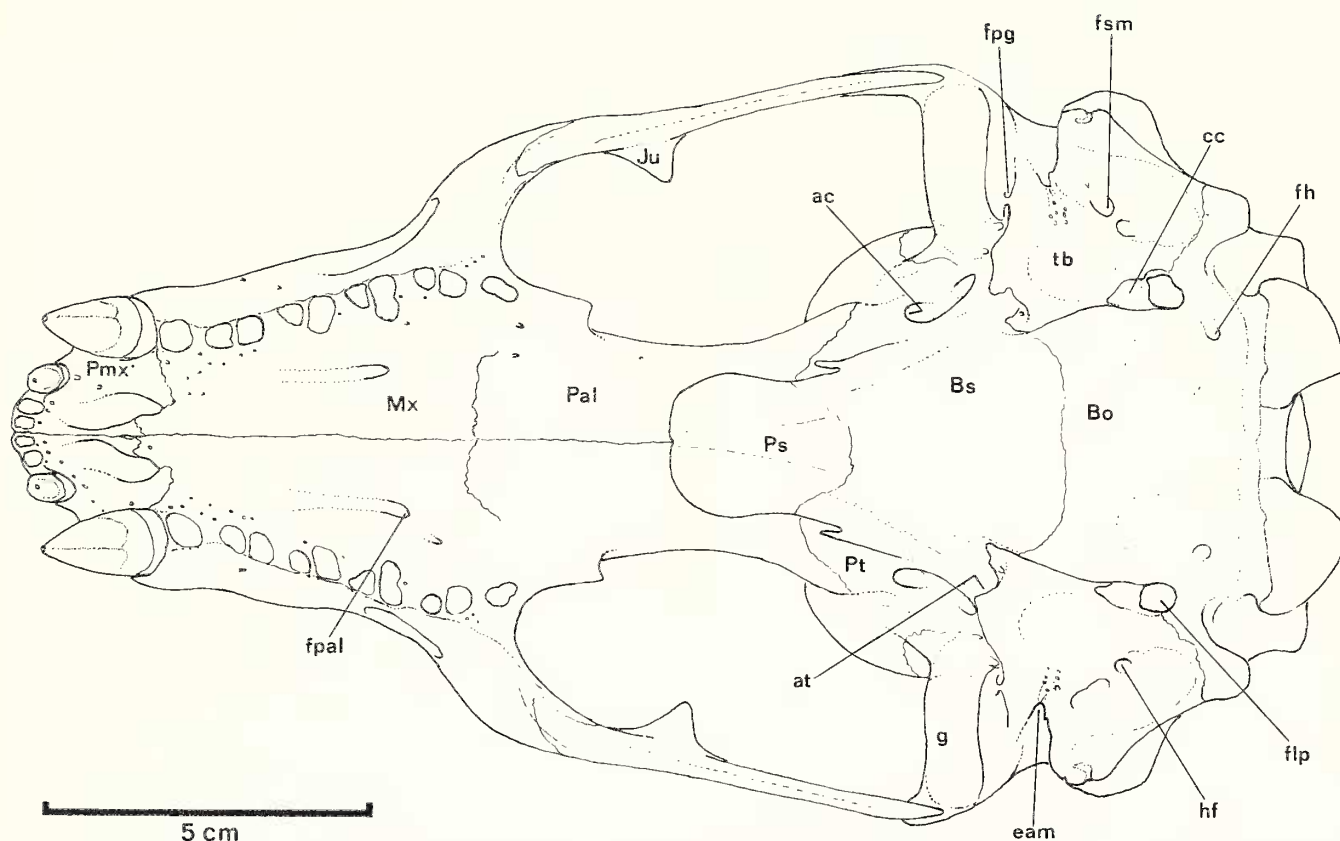


Figure 6. *Pteronarctos goedertae*, new genus and species, restoration of holotype skull, LACM 123883, ventral view; for explanation of abbreviations see Methods and Materials.

I conclude that the individual represented by the holotype was apparently a young adult male on the basis of the following features: the only cranial sutures that are obliterated are the coronal and occipito-parietal, all the others are closed but not fused; the skull yields a suture age of at least 22 by employing the methodology of Sivertsen (1954), thus placing it in the adult age class; the canines are fully erupted, but not heavily worn, with only slight wear on the apex of the right one. I have previously (Barnes, 1979:16) suggested that species of *Enaliarctos* were sexually dimorphic, with female specimens having canines that are 20 to 32 percent smaller than those from males. The canines of the holotype of *P. goedertae* are nearly equal in size to those that have been characterized as the larger dimorph (= males) among canines identified as *Enaliarctos* sp. from near the type locality of *E. mealsi*. Additionally, the holotype skull of *P. goedertae* is larger than the paratype skull of *E. mitchelli*, which was inferred (Barnes, 1979) to have been from a female. The left I³ root of the holotype of *P. goedertae* has a closed pulp cavity at its apex, a further indication that the specimen was an adult. Sectioning one of the teeth might reveal growth layers, but the information that would be derivable at this time from such a procedure probably does not justify destroying anatomical details of the only known specimen of the species.

Pteronarctos goedertae shares with the species of *Enaliar-*

tos the following characters. The palatines extend posteriorly from the palate and, connecting with the pterygoids, form a short tube that surrounds the ventral part of the choanae. The posterior margin of the palate is excavated in a broad U-shape beneath the choanae. There is a squared pterygoid process at the margin of the infraorbital plate of the maxilla. The lateral side of the strut formed by the pterygoid (spanning between the side of the palate and the braincase) is narrow and convex rather than wide and concave as in, for example, *Pinnarctidion bishopi* and imagotariines. The basioccipital bone between the ear regions is narrow anteriorly and relatively wider posteriorly, and encloses on either side an inferior petrosal venous sinus. The paroccipital process is small, posteriorly directed and joined to the mastoid process by a thin crest. The optic foramina are joined in an elongate chiasma as they extend anteriorly from the braincase into the interorbital septum and become separate only relatively far anteriorly within the septum. The optic foramina open into the orbit relatively high above the choanae rather than low, at the anterior edge of the braincase as various other pinnipeds. The medial walls of the orbits bear no vacuities but, instead, consist of solid sheets of bone. The posterior lacerate foramen is relatively small for a pinniped and expanded slightly in an anteroposterior direction rather than transversely as in *Pinnarctidion bishopi* and *Allodesmus* spp. The

Table 1. Measurements (in mm) of the holotype skull of *Pteronarctos goedertae*, new genus and species. See Methods and Materials section for methods of measurements.

Total length	207.5
Postpalatal length (palatal notch to basion)	93.5
Basion to anterior edge of zygomatic root (18)	133.0
Length of tooth row, C to M ²	70.5
Width of rostrum across canines (12)	46.0
Width of palate across anterior alveoli of P ⁴	48.5
Width between infraorbital foramina	54.0
Width across antorbital processes (5)	54.5
Width across greatest interorbital constriction (6)	34.0
Width across supraorbital processes (7)	34.5
Width across greatest intertemporal constriction	22.5
Width of braincase at anterior edge of glenoid fossa (8)	68.0
Zygomatic width (17)	119.5
Auditory width (19)	92.5
Mastoid width (20)	(106.0)
Paroccipital width	76.0
Greatest width across occipital condyles	52.0
Greatest width of anterior nares	29.0
Greatest height of anterior nares	23.0
Width of zygomatic root of maxilla (14)	12.0
Greatest width of foramen magnum	25.5
Greatest height of foramen magnum	16.0
Transverse diameter of infraorbital foramen	12.0

hypoglossal foramen is small and located close to and posteromedial to the posterior lacerate foramen; its opening faces that foramen. The tympanic bulla is most inflated in its central part and its surface is smooth, rather than being rugose or penetrated by numerous vascular foramina as in some species in the subfamily Otariinae. A small postglenoid foramen lies between the bulla and the postglenoid process. Ventral to the anterior end of the carotid canal, the ventral margin of the bulla is retracted posteriorly. A deep and narrow intercondylar notch separates the occipital condyles (Figs. 5, 6), which are closely spaced and protrude prominently from the occipital shield. Even though some roots of some of the cheek teeth have coalesced, they still reveal the numbers and positions of roots that were originally separate as in primitive and terrestrial arctoid fissipeds. The medial lobe of the bilobed posterior root on the P⁴ of *P. goedertae* is a vestige of the separate, medial (protocone) root in species of *Enaliarctos*. The infraorbital foramen is visible in ventral view because the root of the zygomatic process of the maxilla does not project beneath it anteriorly. The orbit is relatively small compared with more derived pinnipeds, but it is relatively larger than in terrestrial carnivores. The postorbital process of the jugal is low and triangular and projects dorsomedially into the orbit. The slender, pointed anterior tip of the zygomatic process of the squamosal terminates considerably posterior to the postorbital process of the jugal. The cheek portion of the maxilla swells outward, unlike the

condition in *Allodesmus* spp. and *Pinnarctidion*, in which the cheek portion of the maxilla retreats dorsomedially from the lateral edge of the cheek tooth row. The manner in which the nasals and maxillae meet the frontals is different in the various groups of otarioids. As in *Enaliarctos* spp., the posterior ends of the nasals of *Pteronarctos goedertae* are relatively wide. They are not narrow and tapered as in *Allodesminae*, and they do not diverge posteriorly as in *Otariinae*. The frontals extend anteriorly on either side of the nasals, separating them for a short distance from the posterior (or frontal) processes of the maxillae. There is a low, narrow sagittal crest, as is characteristic of male individuals of various otariid species, extending from approximately the middle of the interorbital region to the nuchal crest. Some of the above characters may also be found in at least some other species of fossil or living otariids, but they occur together only in the species of *Enaliarctos* and *Pteronarctos*. This fact will have relevance to later inferences that these two genera undoubtedly shared a close common ancestry. Most of the above character states are also primitive for the otariids.

There is also another suite of characters, some primitive and some derived, that is possessed by *Pteronarctos goedertae* and which differentiates it from *Enaliarctos mealsi* and *E. mitchelli*. This suite of characters is summarized in Table 2 and includes the following. The facial angle (cf. Repenning et al., 1971) is greater (142 degrees) than in either *E. mealsi* (approx. 127 degrees) or *E. mitchelli* (approx. 130 degrees). The narial opening is not so high as in *E. mitchelli*, or so broad and low as in *E. mealsi*, and the anterior end of each nasal has a concave margin. The nasolabial fossa is much less distinct, and the rostrum is less tapered anteriorly than in either *E. mealsi* or *E. mitchelli*. The zygomatic arches do not curve upward so much as in *E. mealsi*, but neither are they as low as those of *E. mitchelli*. The part of the maxilla that joins the ventral part of the zygomatic arch is nearly horizontal, not inclined as in *E. mealsi*, bears a shallow fossa, and its posterior border meets the palate at a point opposite the space between M¹ and M² as in *E. mitchelli*. *Pteronarctos goedertae* differs further in that the infraorbital foramen is more compressed dorsoventrally, and the zygomatic arches do not flare so widely from the skull but project more prominently anterolaterally, forming a cup under each eye. The supraorbital processes are small (Figs. 1, 2) but are nonetheless wider than in both *E. mealsi* and *E. mitchelli*. The postorbital region is narrower than in *E. mealsi*, and this serves to accentuate the greater width of the anterior part of the braincase of *P. goedertae*. The external manifestation of the pseudosylvian sulcus of the brain, as a prominent sulcus on the wall of the braincase in *E. mealsi*, is almost nonexistent in *P. goedertae*. In *P. goedertae*, the nuchal crests extend farther posteriorly and the upper parts of the occipital condyles tilt more laterally than in *E. mealsi*. The foramen magnum is of equal size on the holotypes of these two species, but in *P. goedertae* its opening is peaked dorsally, whereas it is rounded dorsally in *E. mealsi*. That part of the basioccipital between the hypoglossal foramen and the condyles in *P. goedertae* is broader and more convex than in *E. mealsi*.

In *P. goedertae*, the premaxillae join to form a pointed

anterior extremity with a small knob-like apical process anterior to the nares as in derived species of Otariinae. The upper cheek tooth rows are more nearly parallel than in both *E. mealsi* and *E. mitchelli*, but they still retain a slight lateral curvature in the area of P^4 and M^1 (Fig. 6). The upper incisor alveoli form an arcade, and the medial two pair are nearly equal in size, each being approximately one-half the diameter of the alveolus for I^3 . A diastema of 3 mm separates the alveolus of I^3 from that of the canine, and the relative sizes of both this diastema and of the incisor alveoli are similar to the condition in Recent species of Otariinae. The I^3 has a slightly recurved crown and a continuous cingulum on its medial, lateral, and posterior sides. This cingulum is partly obliterated on the lateral side of the right I^3 by a large wear facet that resulted from occlusion with the lower canine. On the unworn medial side of the crown, the cingulum has only a very slight vestige of a cusplule. Such a cusplule is a primitive, ursine-like character and is present (although small) on referred specimens of *Pithanotaria starri*, but absent in living otariines (Repenning and Tedford, 1977:59). This cusplule is present and relatively large on specimens of the primitive imagotariine, *Neotherium mirum* (specimens LACM 98147 and UCMP 82362). The size of this cusplule in *P. goedertae*, the only species of enaliarctine for which the I^3 is known, is therefore intermediate between the most primitive and the most derived conditions found in the Otariidae. The root of this tooth in *P. goedertae* is oval in cross section, the primitive condition, and in this regard resembles the Recent fur seals more than the sea lions, in which the root is round in cross section (Repenning et al., 1971).

The canine crown is slightly compressed transversely and, although the root of the canine is in a slightly procumbent position, the crown is oriented almost vertical to the palate. It has a short crest on the proximal part of its medial side and a longer one on the posterior side that extends the length of the crown. These two crests are linked at their proximal ends by a posterolateral, horizontal cingulum located near the gum line of the enamel. Compared with canines of *Enaliarctos mitchelli* (and possibly also of *E. mealsi*; see Barnes, 1979), this tooth in *P. goedertae* has a more recurved crown and less prominent posterior and medial crests (derived condition).

Before discussing the cheek teeth, it is appropriate to review our understanding of cheek tooth morphology and homology in the otariids. Otariid cheek teeth have been conservatively termed merely as postcanine teeth by some authors (e.g., King, 1964, 1983b; Spalding, 1966; Mitchell, 1968). In fact, Scheffer (1958:16) speculated that the ancestors of otariids possibly never possessed carnassial cheek teeth. The presence of six upper cheek teeth, as in the Enaliarctinae, is demonstrably the primitive condition for Otariidae. In light of our present knowledge of the dentition of the enaliarctines (Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Barnes, 1979), and the fact that the fourth cheek tooth in Recent Otariinae has a deciduous predecessor, there is no reason to doubt that these six teeth are the homologs of P^{1-4} and M^{1-2} of terrestrial fissiped carnivores (see Scheffer and Kraus, 1964:297; Tedford, 1976). Also, these teeth have a

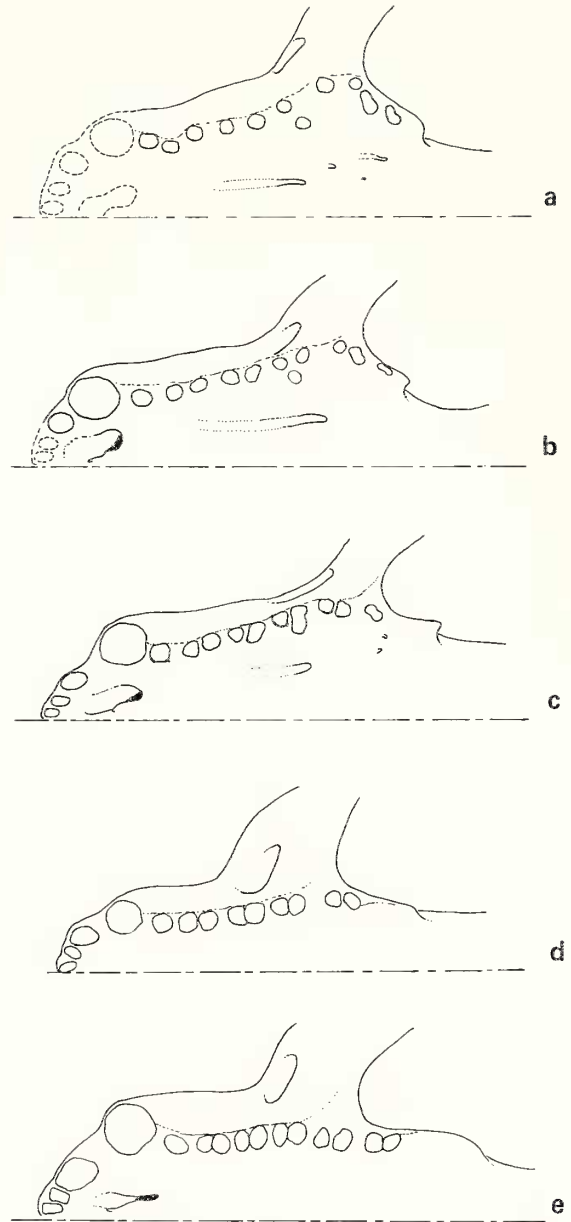


Figure 7. Comparisons of alveoli for teeth and associated palatal structures in five species of primitive Otariidae; a, *Enaliarctos mealsi* Mitchell and Tedford, 1972; b, *E. mitchelli* Barnes, 1979; c, *Pteronarcos goedertae*, new genus and species; d, *Pithanotaria starri* Kellogg, 1925; e, *Thalassoleon mexicanus* Repenning and Tedford, 1977. (a and b from Barnes, 1979; d and e from Repenning and Tedford, 1977.)

basic tritubercular plan (cf. Hershkovitz, 1971), with a reduced talon and protocone, and the major cusp is the paracone.

In the normal dentitions of the more derived fossil and living Otariidae, four, five, or six upper cheek teeth may be present. The exact number is usually species-specific, but in some species it varies between individuals. Progressive evolutionary loss of the M^2 through time in some lineages has

yielded the more derived condition of five upper cheek teeth, and in the case of the living walrus, further loss of M^1 of only four. In the enaliarctines, the most complex upper cheek teeth are the P^4 and M^1 , and these reveal the tritubercular nature of the otariid cheek dentition. In comparison with all of the other species of fossil and living Otariidae, the morphology of these two teeth in enaliarctines is closest to the primitive fissiped cheek tooth morphology and, of these, the P^4 retains essentially a carnassial structure. The crowns of these teeth consist of a major cusp, which is the paracone, a smaller cusp posterior to this, which is the metacone, and a lingual shelf, which is, in part, the protocone. A trigon basin lies between the paracone and the protocone. Although the P^{2-3} of enaliarctines remained premolariform, their morphologies are basically of the typical tritubercular cheek tooth plan whose structures are homologous with those of the P^4 and M^1 (e.g., see Barnes, 1979). In the primitive carnivore condition, there is a separate root above each of the three main cusps. These roots became coalesced or fused to varying degrees in derived lineages of otariid pinnipeds. The roots are still distinct in *Enaliarctos* spp., but in a slightly more derived character state (as exemplified by *Pteronarcos goedertae*), the medial (protocone) root of both the P^4 and M^1 became fused to the posterior (metacone) root. Further root coalescence (fusion) through time in various lineages yielded cheek teeth in some species of otariids with only two roots, or, in a more derived state, a single bilobed root on P^2 to M^2 , and in the most highly derived condition (homodonty), these teeth have a single conical root which is round in cross section. Also, in the advanced stages of homodonty, each cheek tooth crown is comprised principally of a single, large, central cusp, which we now know is the paracone in the upper teeth and the protoconid in the lowers (Mitchell and Tedford, 1973; Barnes, 1979, 1988).

As mentioned above, all of the cheek teeth have fallen out of the holotype specimen of *P. goedertae*; therefore, the following observations are based on empty alveoli. All of its premolar and molar alveoli are larger than those of *E. mitchelli*. P^1 has a single, conical root. P^2 and P^3 each have two roots, arranged anteroposteriorly. The posterior root of P^3 is bilobed, indicating that in *P. goedertae* the ancestral, medial (protocone) root has coalesced with the posterolateral (metacone) root. Similarly, the P^4 has a transversely expanded, even more distinctly bilobed, posterior root. The median lobe of this root is the former protocone root that has coalesced with the one above the metacone, and there is a bridge of root material joining them. In both *E. mealsi* and *E. mitchelli* the protocone root of P^4 is still completely separate. In all three species, the anterior root of P^4 (the one above the paracone) remains separate (Fig. 7a-c). The unknown crown of the P^4 of *P. goedertae* evidently retains a relatively high paracone as the principal cusp; the metacone is evidently very reduced, the protocone reduced to only a small cingulum or shelf at the posterolingual corner of the tooth and probably only a little larger than the comparable cusp on the P^3 of *E. mealsi*.

The progressive posterolateral migration of the medial (protocone) root of P^4 and its ultimate fusion with the pos-

terior (metacone) root in the chronological sequence of the three known species within the genera *Enaliarctos* and *Pteronarcos* serves to partially demonstrate the manner whereby the upper carnassial tooth, inherited from fissiped carnivores via the primitive enaliarctine pinnipeds, became premolariform as the cheek tooth row approached homodonty in derived otariids. However, in *Enaliarctos* the actual morphology of the P^4 crown is known only for *E. mealsi*, in which the crown in occlusal view is an asymmetrical triangle with the protocone reduced and the root above it positioned posteromedial to the large paracone and its root. The small metacone and its root are separate from these, lying more posterolaterally, and forming a drawn out posterior part of the tooth (Mitchell and Tedford, 1973:figs. 5a, 10, 15, 17c; Barnes, 1979:fig. 20a; this paper, Fig. 7a). In *E. mitchelli* the root above the metacone is closer to the root above the paracone, having moved anteromedially so that the three roots, and presumably also the crown, form a nearly equilateral triangle (Barnes, 1979:figs. 4, 5, 20b; this paper, Fig. 7b). The crown of the P^4 of *E. mitchelli* evidently has a more reduced protocone and metacone and a higher, triangular paracone. The anterior displacement of the root above the metacone and the attendant reduction of the posterior part of the P^4 created a diastema between P^4 and M^1 . There are also diastemata between the other cheek teeth of *E. mitchelli*, and these are also characteristic of some of the other, more derived species of otariids.

The M^1 of *Pteronarcos goedertae* has two distinct roots that are more nearly equal in size and are aligned more parallel to the sagittal plane than in either *E. mealsi* or *E. mitchelli*. The posterior root of this tooth, actually two fused roots, is only faintly bilobed and nearly twice the diameter of the anterior one. In *E. mealsi* and *E. mitchelli*, the posterior (fused) root of M^1 lies posteromedial to the anterior root and is distinctly bilobed. In all three species, the medial lobe of the posterior root of M^1 is the relict of the root that was previously above the protocone.

An isolated tooth from California gives some indication of what the M^1 of *P. goedertae* probably is like. This tooth (LACM 126511, Fig. 8b) is from the basal part of the Round Mountain Silt, a part of this rock unit that has been correlated with the Hemingfordian North American Land Mammal Age by Savage and Barnes (1972), is stratigraphically below the richly fossiliferous, Barstovian correlative upper part of the formation, and is approximately contemporaneous with the part of the Astoria Formation that yielded the holotype of *P. goedertae*. The M^1 from California has the correct root morphology to be accommodated by the M^1 alveoli on the holotype: the anterior root is separate and tapered apically, and the posterior two roots are fused into one slightly larger, bilobed root. Characters that this tooth shares with the M^1 of the holotype of *E. mealsi* are a prolonged anterolabial corner, a low and elongate paracone, a small and pyramid-shaped metacone, a notch in the labial margin between these last two cusps, and a protocone represented by a broad shelf. It differs from the holotype of *E. mealsi* in that the anterolingual corner of the tooth is less prominent and the protocone shelf is smaller and situated more posterolingual to the

body of the tooth (Fig. 8). The tooth is too small (crown dimensions: 7.9 mm anteroposteriorly, 5.7 mm wide) to belong to an individual with a skull the size of the holotypes of either *E. mealsi* or *P. goedertae*, and I conclude that it is from a female individual of a species of enaliarctine, possibly a species near *P. goedertae*.

The alveolus for the M² of *P. goedertae* is single but bilobed, obviously resulting from fusion of two roots. The size of the alveolus indicates the tooth was larger than that of either *E. mitchelli* or *E. mealsi*, and in this regard, *P. goedertae* is more like some derived species of Otariinae that have a relatively large M² (Fig. 7e).

A prominent pair of elongate sulci (Figs. 5, 6) are on the palate of *P. goedertae* extending anteriorly from large posterior palatine foramina, which are characteristic of both *Enaliarctos* and *Pteronarctos*. As in *E. mealsi*, there are some smaller foramina scattered posterior to these but, as in *E. mitchelli*, these are fewer and much smaller.

The internal narial opening, flanked by the palatines beneath the choanae in *P. goedertae*, is proportionately shorter than in *Enaliarctos* (the holotypes of *E. mealsi* and *P. goedertae* have the same measurement from the basion to the palatal notch [Table 1]). This condition may be correlated with an anteroposterior shortening of the mid-section of the skull in *P. goedertae*, or may be simply a primitive character.

Other proportional differences in the braincase differentiate *P. goedertae* from *E. mealsi*. In *P. goedertae* the width across the mastoid and paroccipital processes is relatively greater, resulting from enlargement and lateral expansion of these processes as well as from the wider basioccipital and braincase. The wider braincase results in a narrower squamosal fossa, which lies between the braincase and the zygomatic arch. The mastoid and paroccipital processes and the ear region are positioned relatively farther anteriorly on the skull than in *E. mealsi*. This results in a narrower external acoustic meatus, beneath which the lateral edge of the bulla is wrinkled and compressed anteroposteriorly. The anteromedial corner of the tympanic bulla extends medial to the glenoid process in *P. goedertae*, farther anteriorly than it does in *E. mealsi*. This anterior position of the bulla is primitive, as in various fissipeds and in primitive ursids. The more anterior position of the enlarged mastoid and paroccipital processes in *P. goedertae* undoubtedly provided an enhanced mechanical advantage for enlarged neck muscles inserting on them. This certainly has an analog in the derived Recent otariines, in which these processes are large and facilitate powerful and rapid movement of the head and neck during feeding (e.g., Mitchell, 1966:8–9). The ventral ends of the nuchal crest also sweep noticeably farther anteriorly as they approach the paroccipital processes.

I have previously (Barnes, 1979:9, 26) called attention to the existence in *Enaliarctos mealsi* and *Pinnarctidion bishopi* of an apparent embayment in the lateral edge of the basioccipital for an inferior petrosal venous sinus. Such sinuses are also present in fossil Amphicyonidae, in which Hunt (1974: 47–48) has suggested was held a loop of the median branch of the internal carotid artery as in Recent bears. The previously described evidence for these embayments in enaliarc-

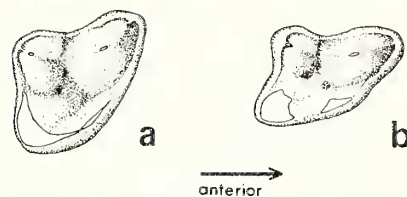


Figure 8. The right M¹ in enaliarctines; a, *Enaliarctos mealsi* Mitchell and Tedford, 1973; b, enaliarctine, near *Pteronarctos goedertae*, new genus and species, LACM 126511, from LACM locality 3386; occlusal views, not to scale. White areas indicate wear facets on the protocone shelf. Arrow indicates anterior. (a, composite based on holotype, LACM 4321 from LACM locality 1627, reversed from Mitchell and Tedford [1973:fig. 10], and referred specimen, UCMP 86211 from UCMP locality V7032 (= LACM 1626), from Barnes [1979:fig. 2j].)

tines is the presence of matrix-filled cavities within the basioccipital dorsal to the tuberosities marking the insertion of the paired *rectus capitis ventralis* muscles (Barnes, 1979:26). To determine whether or not *Pteronarctos goedertae* had such an embayed basioccipital, the bone was cut open on one side of the basioccipital, and a small matrix-infused vacuity was found. This recess is much smaller than in *Enaliarctos mealsi* or *Pinnarctidion bishopi* and seems to be a vestige of the sinus. It demonstrates the persistence of this primitive character in all known enaliarctines.

The area of greatest inflation of the tympanic bulla of *E. mealsi* is in the medial part, but in *P. goedertae* it is in the anteromedial part. The posterior lacerate foramen of *P. goedertae* is smaller and more circular in shape than in *E. mealsi*. The paired fossae on the basioccipital for insertion of the *rectus capitis ventralis* muscles are deeper. The crest that spans between the mastoid and paroccipital processes in *E. mealsi* is low and rounded, but in *P. goedertae* it extends farther laterally and has the form of a thin shelf.

RELATIONSHIPS

Pteronarctos goedertae is very different from the larger and comparatively more derived desmatophocine otariid *Desmatophoca oregonensis*, the only other fossil pinniped to have been described from the Astoria Formation in coastal Oregon. It is also demonstrably different from the other known species in the subfamily Enaliarctinae and can be differentiated from all other named small Miocene otariids. Only the chronologically more recent Middle Miocene species *Neotherium mirum* Kellogg, 1931, is not known by published comparable cranial material. This small otariid, confidently known only from the Sharktooth Hill Bonebed in California (Mitchell, 1961; Mitchell and Tedford, 1973; Repenning and Tedford, 1977), is a primitive member of another subfamily, the Imagotariinae (synonymized and included within the Dusiagnathinae by Repenning and Tedford [1977:54–55]). Originally named on the basis of foot bones, additional, and as yet unpublished, topotypic material of *N. mirum* now includes many postcranial bones and skull parts. Presently under study by the author, these demonstrate that *N. mirum* is

Table 2. Differences between *Enaliarctos mealsi* Mitchell and Tedford, 1973, *E. mitchelli* Barnes, 1979, and *Pteronarctos goedertae*, new genus and species.

<i>Enaliarctos mealsi</i>	<i>Enaliarctos mitchelli</i>	<i>Pteronarctos goedertae</i>
1. Four posterior palatine foramina on each side of palate, palatine sulcus present.	1. One foramen on each side of palate continuous with long sulcus.	1. One foramen on each side, continuous with long sulcus.
2. Ventral surface of zygomatic arch beneath infraorbital foramen is inclined anterodorsally and lacks fossa.	2. Surface more horizontal, with fossa	2. Surface more horizontal, with fossa
3. External narial opening wide and very low, nearly oval in anterior view.	3. Narial opening higher, nearly circular in anterior view.	3. Narial opening low, sloping, nearly circular in anterior view.
4. Lateral (cheek) surface of maxilla strongly convex.	4. Lateral surface more vertical, less convex.	4. Lateral surface strongly convex.
5. Posterior border of zygomatic arch joins palate opposite middle of M ¹ .	5. Posterior border joins palate opposite space between M ¹ and M ² .	5. Posterior border joins palate opposite space between M ¹ and M ² .
6. Rostrum flattened dorsoventrally.	6. Rostrum arched dorsoventrally.	6. Rostrum slightly flattened.
7. Posterolabial root of P ⁴ widely separated from the other two roots.	7. Three roots of P ⁴ nearly equidistant and forming nearly equilateral triangle.	7. Two posterior roots of P ⁴ coalesced, anterior root separate.
8. Nasal bones slope anteroventrally.	8. Nasal bones not sloping, nearly horizontal.	8. Nasal bones sloping slightly.
9. Zygomatic arch has continuous dorsal curvature in lateral view.	9. Zygomatic arch flatter, not curved dorsally as much as in <i>E. mealsi</i> .	9. Zygomatic arch flatter, not curved dorsally.
10. M ² alveolus tiny.	10. M ² alveolus tiny.	10. M ² alveolus large, bilobed.
11. Embrasure pit on maxilla for M ₁ deep.	11. Embrasure pit moderately deep.	11. Embrasure pit shallow.
12. Tympanic bulla most inflated centrally.	12. Not known.	12. Tympanic bulla most inflated anteriorly.
13. Crest between mastoid and paroccipital processes low, rounded.	13. Not known.	13. Crest thin, projecting laterally.

distinct from *P. goedertae*. *Pteronarctos goedertae* differs cranially from *N. mirum* (on the basis of referred specimens: UCMP 82362, 82363, 86132 and LACM 52172, 98147, 127696) by having a more inflated bulla extending farther anteriorly beneath the median lacerate foramen; a mastoid process which is not so cuboid in shape and is located farther anteriorly on the basicranium and constricting the external acoustic meatus; a narrower paroccipital process; a larger postglenoid foramen located in a transverse groove; no pre-glenoid process and a shallower glenoid fossa; a foramen ovale more covered by the pterygoid in ventral view; a rounded medial edge of the bulla; a smaller P¹ alveolus; no adventitious medial root on the P²; a smaller vestige of the medial (protocone) root on P³; a more posteriorly located medial (protocone) root and a distinctly separate anterior (paracone) root on P⁴; a more prominent sulcus on the palate extending anteriorly from the anterior palatine foramina; a greater facial angle; more procumbently rooted, smaller upper canines with round roots; and a smaller optic foramen that is located more dorsally in the interorbital region.

The Late Miocene fur seal-like otariine pinniped *Pithanotaria starri* is geologically younger than any of the above taxa. The holotype and referred specimens (Repenning and Tedford, 1977:58–60, pl. 19) of this species show it to differ from enaliarctines by having essentially a homodont cheek dentition, a nearly straight upper cheek tooth row, and two-rooted P^{2–4} and M¹, and by lacking the M². All other named otariids belong in different subfamilies and are clearly mor-

phologically different from *Pteronarctos goedertae*, are of different ages, and, in most cases, are much larger in body size.

Many character states of *Pteronarctos goedertae* are more derived than those of both *Enaliarctos mealsi* and *E. mitchelli*. *Pteronarctos goedertae* could not have evolved from either of the latter species, however, because it also has other characters that are more primitive in comparison with both of them, and each of these three species has its own combination of unique derived (autapomorphic) characters. Within the Jewett Sand in Kern County, California, specimens of *E. mitchelli* have only been found in stratigraphically higher, and therefore geochronologically younger, rocks than *E. mealsi*. *Enaliarctos mealsi* could have been ancestral to *E. mitchelli* (see Barnes, 1979). Despite its more derived characters and more recent age relative to *E. mealsi*, *E. mitchelli* is not morphologically intermediate between that species and *P. goedertae*. Its unique derived characters, compared with *E. mealsi* (and *P. goedertae*) include, among others, incisive foramina that pass more vertically from the palate into the external nares, upper cheek teeth whose roots are relatively smaller, fusion of the two roots of M² into one tiny bilobed root, a relatively large orbit, a lesser facial angle, and a larger narial opening.

Compared with *E. mealsi* (and with some of the known characters of *E. mitchelli*) the different suite of derived characters (i.e., those that are more like species of Otariinae) of *P. goedertae* are: straighter upper cheek tooth rows, P⁴ with its posterior two roots coalesced suggesting a reduction of the

protocone (and therefore, also a reduction of the carnassial function of the tooth), M^1 with more nearly equal-sized anterior and posterior roots, reduced embrasure pit on the palate between P^4 and M^1 indicating a corresponding reduction in size of the lower carnassial (M_1), ventral part of zygomatic process of the maxilla ventral to infraorbital foramen more nearly horizontal, zygomatic arch straighter and less arched in its lateral part, larger supraorbital process of the frontal, shallower nasolabialis fossa anterior to the orbit, narrower posterior part of the interorbital area, more prominent anterolateral corners of the braincase, and the shallower sulcus on the lateral wall of the braincase marking the pseudosylvian sulcus of the brain. Despite the presence of its otherwise more derived characters, *P. goedertae* is more primitive than both of the species of *Enaliarctos* by virtue of having a shorter posterior extension of the palate ventral to the choana, a smaller posterior lacerate foramen, a bilobed posterior root on P^3 representing a remnant relic of the medial (protocone) root, and a large M^2 alveolus (Fig. 7). The evidence from the characters cited above, therefore, indicates that within the subfamily Enaliarctinae there were at least three different evolutionary lineages, represented by the genera *Enaliarctos*, *Pteronarctos*, and *Pinnarctidion*, and that the youngest known species, *P. goedertae*, must have evolved from a taxon that was even more primitive than the earliest and most primitive species, *E. mealsi*.

Certain derived characters of *P. goedertae* are also present in the various living species of fur seals in the relatively primitive otariine genus *Arctocephalus* (see Repenning et al., 1971; Bonner, 1981), and these and other shared characters support the idea that the subfamily Otariinae evolved from, or shares its ancestry with, some species of Enaliarctinae. Such characters are: palatine bones that form a short tube at the back of the palate ventral to the internal nares; a small paroccipital process that is connected to the mastoid process by a slender crest; a posterior lacerate foramen that is expanded anteroposteriorly rather than transversely; optic foramina that join within the interorbital septum and that exit at a relatively elevated position within the orbits; occipital condyles that project prominently posteriorly and are closely spaced and separated by a narrow and deep intercondylar notch; a cheek portion of the maxilla with a convex lateral surface that projects outward (laterally) beyond the palatal margin; a dorsal margin of the anterior part of the zygomatic arch that is flared upward and outward over the infraorbital foramen to form a flange that cupped the front of the eye; pterygoid struts that connect the palatine and the basiteranium that are elongate, nearly parallel, and convex on their lateral sides; tympanic bullae that are inflated medially and anteriorly; nuchal crests that are curved and flaring posteriorly over the occipital shield; a low sagittal crest that extends from the posterior part of the interorbital area to the occipital crest; a postorbital process of the jugal that is high, triangular, bent inward (medially) toward the orbit, and separated from the anterior tip of the zygomatic process of the squamosal; and posterior ends of the nasal bones that are short, tapered, and closely appressed and penetrating between frontals, but slightly diverging so that there is an ir-

regular transverse line created by the suture between the frontal and the rostral bones (maxillae and nasals).

Mitchell and Tedford (1973) did not specifically propose relationships between *Enaliarctos* and any other type of otariid. Mitchell (1975) later considered the subfamily Enaliarctinae as an extinct lineage with an origin near that of modern fur seals and sea lions, the subfamily Otariinae. Subsequently, Repenning and Tedford (1977) and Barnes (1979) interpreted the genus *Enaliarctos* as being directly ancestral to both the fur seals and sea lions. No appropriate fossils had been described, however, that represent this lineage during the approximately 14 million year hiatus between the youngest known species of *Enaliarctos*, *E. mitchelli*, at approximately 24 to 25 m.y.a., and the oldest fur seal-like pinniped, *Pithanotaria starri* Kellogg, 1925, which lived about 11 m.y.a. (Repenning and Tedford, 1977:fig. 6). *Pteronarctos goedertae* is morphologically a better ancestor of the Otariinae than any species of *Enaliarctos* and now provides the opportunity to document animals apparently belonging on or near this lineage that were alive approximately 19 m.y.a.

CLASSIFICATION OF THE OTARIIDAE

FAMILY GROUP NAMES

Proposed classifications of otariid pinnipeds have varied among recent authors (see Barnes et al., 1985:table 1). The arrangement that I use in this paper is based on that proposed by Mitchell (1968, 1975) and on the one that I used in 1979. I recognize one family, the Otariidae, rather than two (Otariidae and Odobenidae, e.g., Scheffer, 1958; King, 1983a; Enaliarctidae and Otariidae [including Odobeninae], Tedford, 1976:table 1) or four, as has been proposed by Repenning and Tedford (Repenning, 1976; Repenning and Tedford, 1977 [Enaliarctidae, Desmatophocidae, Odobenidae, and Otariidae]). The classification used by Repenning and Tedford served to maintain the ranks as then used by most neontologists. It is significant that these ranks have now been revised by some (e.g., Hall, 1981) to reflect the fossil evidence, and thus, the ranks used by Repenning and Tedford may be reconsidered. The differences between these classifications are principally ones of rank and hierarchy, however, rather than of implied interrelationships. They all recognize the sea lions and walruses in a pinniped group, with variously related fossil relatives, and it is a commonly accepted notion that the group is monophyletic (Mitchell and Tedford, 1973: 278–279; Mitchell, 1975; Repenning, 1976; Tedford, 1976; Repenning and Tedford, 1977; Barnes, 1979; King, 1983a). In light of this and the relatively recent (middle Cenozoic) origin and diversification of the group, I believe that the recognition of several subfamilies within a single family, the Otariidae, is taxonomically more conservative and brings more balance to the classification in the context of the systematics of the order Carnivora. Among the other large group of (relatively distantly related [e.g., see Tedford, 1976]) pinnipeds, the true seals, approximately equal morphological diversity has been accommodated in recently published classifications within one family, the Phocidae. For example, despite the extensive morphological differences between the

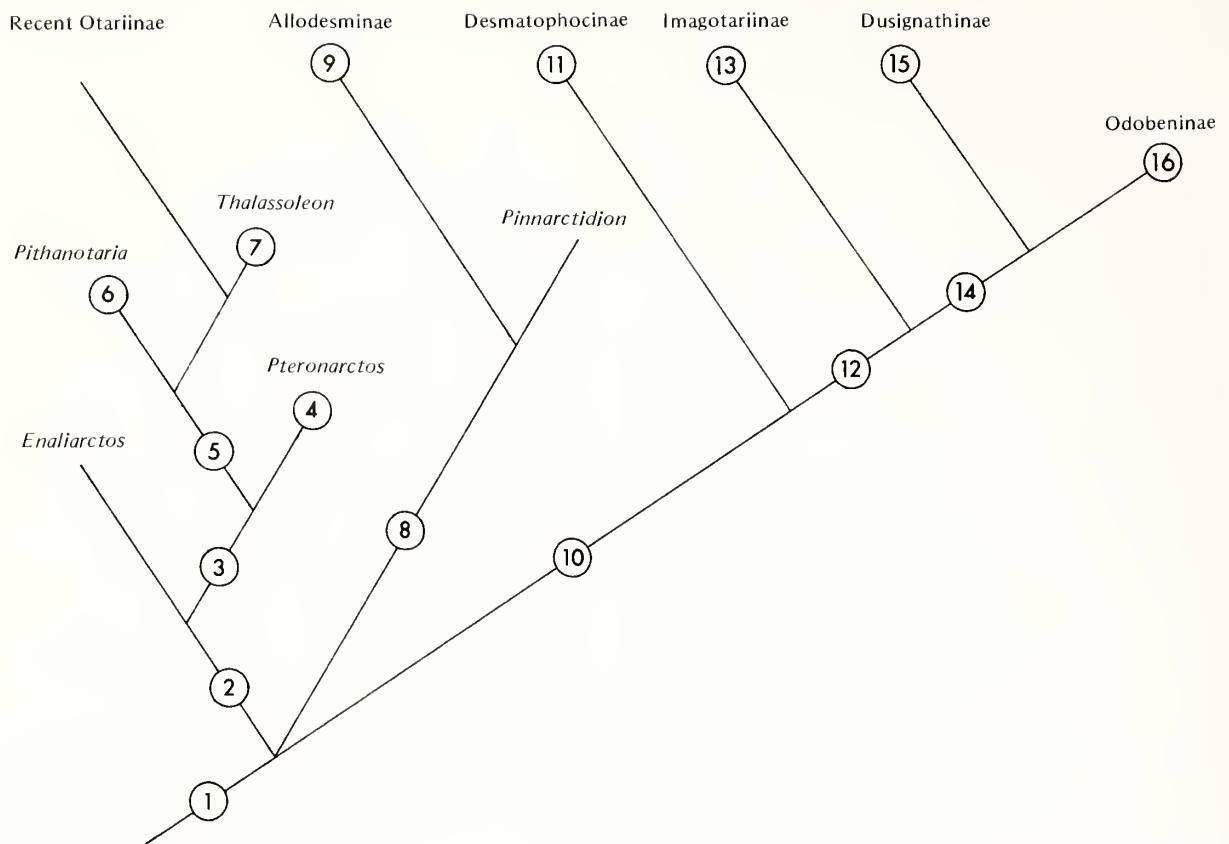


Figure 9. Cladogram showing relationships of otariid genera. Characters marking dichotomies are as follows: 1) Neck lengthened; proximal limb elements shortened; maxilla forming part of wall of orbit; foramen rotundum and anterior opening of alisphenoid canal combined into one large orbital fissure; foramen ovale and posterior opening of alisphenoid canal joined in an elongate recess; sphenopalatine foramen enlarged; petrosal isolated from surrounding cranial bones; embayment formed in lateral edge of basioccipital for loop of median branch of internal carotid artery; mastoid process large and cubic in shape; basal whorl of cochlea directed posteriorly; head lost from incus; auditory ossicles not enlarged; entotympanic restricted to medial part of bulla around carotid canal; internal acoustic meatus round; posterior lacerate foramen enlarged, not expanded transversely; bony tentorium in braincase closely appressed to dorsal surface of eminence containing semicircular canals and floccular fossa; postglenoid foramen reduced; entepicondylar foramen lost from humerus; olecranon process of ulna enlarged; aquatic propulsion by forelimb as well as hind limb, principally by forelimbs (family Otariidae). 2) Posterior end of nasal bones shortened, blunt, marked by irregular sutures; pterygoid strut between braincase and palate rounded, inflated on lateral surface; sagittal crest prominent on braincase, especially so in male individuals; maxilla dorsal to infraorbital foramen projecting farther anteriorly than that below the foramen. 3) Bulla flattened; anterior septum in tympanic cavity reduced; preglenoid process reduced; fossa on braincase wall marking pseudosylvian sulcus of brain reduced; protocone reduced on P^4 and M^1 . 4) Cheek tooth rows more nearly parallel, protocone shelf of P^4 reduced, roots of P^4 reduced to two with posterior two roots fused, posterior part of interorbital area narrow, preglenoid process lost, fossa corresponding to pseudosylvian sulcus shallow (*Pteronarctos*). 5) Anterior border of orbit flared outward dorsal to infraorbital foramen to create a cup beneath the eye; orbital vacuity forms; interorbital septum compressed causing right and left optic foramina to be joined; cheek teeth homodont, central cusp on crown emphasized, accessory cusps and cingulae reduced; cheek tooth rows parallel or nearly so; posterior upper cheek teeth with two roots; supraorbital process of frontal enlarged and projecting laterally; embayment in lateral edge of basioccipital for loop of median branch of internal carotid artery lost; occipital condyles nearly parallel, high on skull; paroccipital process thick, knob-like; basioccipital relatively narrow and nearly parallel-sided; tympanic membrane reduced in diameter; tympanic crest reduced, not projecting prominently into tympanic cavity; bony tentorium in braincase closely appressed to dorsal surface of eminence containing semicircular canals and floccular fossa; fossa for origin of tensor tympani muscle lost (both presumed in *Pithanotaria*); forelimb rotated into position parallel to sagittal plane; deltoid tuberosity of humerus included within deltoid crest; olecranon process of ulna expanded and projected proximo-posteriorly; trochanteric fossa of femur lost (subfamily Otariinae). 6) M^2 lost, P^4 - M^1 diastema present (*Pithanotaria*). 7) M^2 lost; tibia and fibula fused at proximal end (except *T. macnallyae*) (*Thalassoleon*). 8) Palate broad, relatively flat; wide spaces between cheek teeth; paroccipital process enlarged; pterygoid process of maxilla ventral to orbit thin and expanded laterally; choana wide, dorsoventrally compressed; optic foramen posteroventrally located ventral to anterior end of braincase; anterior lacerate foramen (= orbital fissure) bilobed and large; epitympanic recess enlarged; auditory ossicles enlarged; posterior lacerate foramen expanded transversely; internal acoustic meatus broad, dorsoventrally flattened, bilobed, with canals for facial and vestibulocochlear nerves separated by low septa; postorbital process of jugal extended dorsally and applied to anterior end of zygomatic process of squamosal. 9) Cheek teeth homodont, with reduced cingulum and accessory cusps, and bulbous crowns; carinae lost on canine crowns; zygomatic process of squamosal expanded dorsoventrally; orbit enlarged; orbital vacuity forms; interorbital septum compressed causing optic foramina to merge; dorsal margin of zygomatic arch anterior to orbit retracted dorsal to infraorbital foramen;

primitive monk seals (*Monachus* spp.), the derived Antarctic seals, the giant elephant seals (*Mirounga* spp.), and the small harbor seals (*Phoca* spp.) and related taxa, they are classified in separate subfamilies within the family Phocidae (e.g., see de Muizon, 1982; King, 1983a:10). I consider such morphological differences to be of a magnitude commensurate with those between the walruses (*Odobenus rosmarus*) and the fur seals (e.g., *Arctocephalus* spp. and *Callorhinus ursinus*).

In any phylogenetic analysis or classification that includes fossils as well as Recent taxa, the only comparable characters that are now universally comparable and testable by repeated observation are those based on osteology. To ignore a rich fossil history of any animal group is to lose valuable and interesting insights into a wealth of information that is applicable to studies of systematics, distribution, behavior, and population structure of the living descendants. In this context, walruses have been shown not to be evolutionarily very far from other otariids but to have evolved some of their extreme morphological specializations in only quite recent geological time and to share other diverse characters with both extinct and surviving otariid groups (Mitchell, 1966, 1968, 1975; Barnes, 1972, 1979; Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Barnes et al., 1985:fig. 6).

King (1983a:15) presented a table of characters differentiating the superfamilies Phocoidea (true seals) and Otarioidea (sea lions and walruses), groups which, for the present study, can be equated with the families Phocidae and Otariidae, respectively. Another table (King, 1983a:17) purports

to differentiate three families, Phocidae, Otariidae, and Odobenidae, on the basis of some often-cited neontological characters, some of which the odobenids appear to share in different combinations with both of the other families. The problem with this approach is that it does not accommodate any of the extinct groups (the various subfamilies I recognize, or the families Enaliarctidae and Desmatophocidae of some authors; see King, 1983a:136); it relies in part on characters of the soft anatomy which are not determinable from the fossil record, and it includes some osteological characters that are reputedly diagnostic for otariids and odobenids, but which are not valid for even the closely related and geologically relatively recent fossil representatives of each group. For example, some of the osteological characters that King lists to characterize a family Odobenidae (enlarged upper canines, upper incisors without transverse grooves, lower incisors absent, and mandibular symphysis fused in adults) serve to exclude from that family virtually all of the diverse fossil members that were assigned to it by Repenning and Tedford (1977). Most of the remainder of the list of osteological and dental characters King listed can also be used to define species of Enaliarctinae and Allodesminae. It is clear from King's text and phylogeny that she recognizes the diverse fossil otariid groups that have been documented by paleontological studies; the problem lies in her choice of limited characters of only living taxa to characterize groups that have known fossil members.

Wyss (1987) presented a study, nominally to compare the

interorbital region elongated; embayment in lateral edge of basioccipital for loop of median branch of internal carotid artery lost; tympanic membrane reduced in diameter; tympanic crest of low relief, not projecting into tympanic cavity; auditory ossicles greatly enlarged; fossa for origin of tensor tympani muscle lost; facet for tympanohyal within hyoid fossa well developed; dentary flattened with elevated condyle and expanded angle; manus rotated into sagittal plane; bones of manus and pes thickened and flattened; deltoid crest of humerus elongated; deltoid tuberosity included within crest; proximal end of ulna bent posteriorly; olecranon process of ulna thickened; lesser trochanter of femur reduced; carpals and tarsals bulbous, with flattened articular surfaces; aquatic propulsion principally by forelimbs (subfamily Allodesminae). 10) Fossa on braincase wall marking pseudosylvian sulcus of brain reduced; tympanic bulla flattened, wrinkled; embayment in lateral edge of basioccipital for loop of median branch of internal carotid artery lost; fossa for origin of tensor tympani muscle lost; carnassial function lost. 11) Orbit enlarged; cheek tooth crowns bulbous, with smooth enamel; paroccipital process enlarged; tympanic crest reduced, not projecting into tympanic cavity; pterygoid process of maxilla expanded laterally beneath orbit (subfamily Desmatophocinae). 12) Hyoid fossa positioned posterior to tympanic bulla; auditory ossicles enlarged; occipital condyles widely flaring and positioned relatively low on cranium; paroccipital process reduced, thin and plate-like; mastoid process enlarged, crescentic in shape; optic foramina retracted to ventral position beneath anterior end of braincase; basioccipital broad, expanded posteriorly; bony Eustachian canal enlarged; internal acoustic meatus broad, dorsoventrally flattened, bilobed, with canals for facial and vestibulocochlear nerves separated by low septa; auditory ossicles enlarged; radius and ulna shortened; distal end of radius expanded, with large radial crest and radial process; pit or rugosity marking attachment of pollicle extensor muscle located on dorsal surface of metacarpal 1; metacarpal 1 curving laterally; trochanteric fossa of femur lost; lesser trochanter of femur large; prominent tuberosity on medial side of calcaneal tuber. 13) Sagittal crest moderately developed; tympanic membrane slightly reduced in diameter (membrane-to-oval window ratio approximately 10:1); cheek teeth with broad principal cusp, small anterior and posterior cusps, prominent cingulae; attachment for pollicle extensor muscle on metacarpal 1 in the form of pit; femur widened transversely, with enlarged lesser trochanter, and distal trochleae facing posteriorly (subfamily Imagotariinae). 14) Anterior cheek teeth with round, single roots; palate transversely arched; mandibular symphysis elongate, sloping posteroventrally; ventral border of dentary nearly horizontal; angle of dentary reduced, concavity in margin posterior to genial tuberosity. 15) Tooth enamel thin; cheek teeth with bulbous crowns and reduced cingular and accessory cusps; upper and lower canines elongate, slender, but not tusk-like; lower incisors greatly reduced or lost; M₂ lost; dentary short, thin transversely, with posterior end bent dorsally, and diverging abruptly from sagittal plane; humerus, radius, and ulna shortened and thickened; humerus with elongate, thick deltoid crest, large entepicondyle, distal trochlea canted obliquely dorsomedially, distal end compressed anteroposteriorly and expanded transversely, lesser tubercle lower than head (subfamily Dusingathinae). 16) Lower canine reduced; upper canine enlarged; M₂ lost; sagittal crest lost; nuchal crest reduced; lacrimal process enlarged; posterior ends of nasal bones bluntly terminated, aligned with transverse suture between frontals and maxillae; zygomatic process of squamosal blunt, reduced; zygomatic process of jugal (including the postorbital process and part of maxilla) expanded dorsoventrally; I¹ reduced or lost; M₂ lost; attachment for pollicle extensor muscle on metacarpal 1 in the form of a rugosity (subfamily Odobeninae).

ear region of walruses with those of other pinnipeds, but considered a variety of other morphological characters, and concluded that all fossil and living pinnipeds form a monophyletic group. This conclusion is contradictory to that reached by many other researchers who have examined many of the same characters as Wyss, and the work deserves a more detailed reply than can be provided here. Wyss further concluded that the family Otariidae includes only the fur seals and sea lions, is the most primitive group of living pinnipeds, and has apparently close but unspecified relationships with enaliarctines. The enaliarctine *Pinnarctidion* and the Desmatophocinae and Allodesminae he concluded have little relationship with Otariidae but close relationships with the Phocidae, which he also concluded are closely related to the walruses.

A few key points call Wyss' conclusions into question. He (1987:21, table 2) concluded that the lack of large supraorbital processes in various pinniped groups is derived. In fact, just the opposite is the case. Absence of the processes is shown by the fossil record to be primitive. Large processes evolved, as a unique derived character, in only one pinniped group, the Otariinae (fur seals and sea lions), and the enlargement does not show up in the fossil record until Late Miocene time. Wyss also cited a "mortised" squamosal-jugal articulation in the zygomatic arch as being a shared derived character that links phocids, *Allodesmus* (with which he included the demonstrably separate Desmatophocinae), and *Pinnarctidion*. The structure being referred to is an anteroposterior thickening and dorsal extension of the postorbital process of the jugal and a dorsoventral expansion of the anterior end of the zygomatic process of the squamosal. This modification has evolved in *Pinnarctidion*, *Allodesmus*, Phocidae, Odobeninae (not listed by Wyss), and also in unrelated Sirenia and Desmostylia, among other marine mammals. Among these various groups, and even among the four pinniped groups cited, the ways in which the bones are modified and the extent of their modification is highly variable. This should indicate clearly that the modification is a convergent derived character and should be suspect in phylogenetic analyses.

One of the most complete statements of the diversity of characters and the distribution of them among the various fossil and living otariid groups can be found in the work of Mitchell (1968:1893–1896, table V). Although it is not easy at first to sort out the critical diagnostic characters in his study, it clearly points out how the many types of fossil and living otarioid pinnipeds possess partially overlapping suites of characters. For example, the extinct and relatively derived species in the subfamily Allodesminae share both primitive and derived cranial characters in common with the Odobeninae but have aspects of their highly derived limb morphology that are convergent with the Otariinae, and the extinct species of Imagotariinae share some postcranial and basicranial characters in common with species in the Odobeninae and have some dental and mandibular features shared in common with the extinct Enaliarctinae and others that are convergent with some of the Recent Otariinae. Greatly enlarged canine tusks and the accompanying extreme rostral modifications are important derived characters of the living

walruses but are relatively recently acquired, as attested by the discovery of fossil relatives, such as *Aivukus cedrosensis* Repenning and Tedford, 1977, which are less modified (Barnes et al., 1985). Among other mammals (e.g., Monodontinae [narwhals] in the cetacean family Monodontidae, and Machaerodontinae [saber tooth cats] in the carnivore family Felidae), the presence of enlarged anterior teeth and the concomitant derived modifications of the rostrum are commonly reflected in published classifications as subfamilial rather than as familial differences.

Some of the otariid subfamilies are now known to have had considerably earlier origins (Barnes, 1979:fig. 22) than had been indicated previously (Mitchell, 1975:fig. 1; Repenning and Tedford, 1977:fig. 6), and the Early Miocene species of Enaliarctinae are now known to have been relatively diverse. A broad spectrum of taxa, including walrus-like and sea lion-like animals and many with intermediate character suites, are now known to have existed. If all of these early otariids were to be given equal taxonomic status, based on similar levels of morphological distinctions, the suprageneric groups would become too numerous to be useful (witness Dubrovo's [1981] Kamtschatarctinae; see Barnes et al., 1985: 36, 38).

Tedford (1976) reviewed the evidence for relationships of both otariid and phocid seals within the context of the order Carnivora. He summarized evidence that otariids had an origin from terrestrial fissiped carnivores separate from that of phocids. On the basis of a cladistic analysis, he classified both phocids and otariids in the carnivore infraorder Arctoidea (in contrast to Cynoidea and Feloidea), but, underscoring the pinniped diphyly, he classified the Otariidae (and the superfamily Otarioidea) in the parvorder Ursida with bears, and the Phocidae in the parvorder Mustelida with mustelids in the superfamily Musteloidea. Ginsburg's (1982) arrangement is similar to that of Tedford's, except that he used infraorders instead of parvorders. He classified the family Ailuridae (lesser pandas) within the infraorder Ursida and considered it to be the sister-group of Otariidae as well as the Ursidae but did not join the latter two in a higher category. For several reasons, therefore, I have used Tedford's suprafamilial categories.

The characters differentiating the various subfamily groups of otariids (Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, Dusingathinae, and Odobeninae) in the classification that I present here have been documented previously (Mitchell, 1968, 1975; Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Barnes, 1979) and need not be repeated. The Imagotariinae and Dusingathinae are the least easy to differentiate and were synonymized by Repenning and Tedford (1977). I have kept them separate because of the distinctive features of the type genus of each subfamily. Each of the subfamilies has a unique combination of primitive and derived characters, although some characters are shared among different groups. Dubrovo's (1984) attempts to rediagnose the Otarioidea (= my use of Otariidae) and Enaliarctidae (= Enaliarctinae) are neither as accurate nor as useful as those that have been provided in the earlier publications cited above.

SUBFAMILY ENALIARCTINAE

Following the treatment of Repenning and Tedford (1977), I continue to recognize the primitive subfamily Enaliarctinae as a horizontal group, a grade rather than a clade, because it includes taxa from which at least two (and undoubtedly other) later otariid lineages apparently evolved (Fig. 9; Repenning and Tedford, 1977; Barnes, 1979; Barnes et al., 1985; fig. 6). Repenning and Tedford (1977) defined the group, in part, using an arbitrary morphological feature: the retention of the primitive carnassial structure of the cheek teeth P^4 and M_1 from the terrestrial fissiped carnivore ancestors. Recognition of the subfamily Enaliarctinae does have taxonomic utility at the present time, however, considering the still comparatively meager state of our knowledge of early otariid evolution. Its use is analogous to that of the Hyracotheriinae among the Perissodactyla. Considering the established relationships, it might very well be appropriate to assign *Enaliarctos* and *Pteronarctos* to the subfamily Otariinae. It would be difficult at the present time, however, to decide if *Pinnarctidion* is closer to the Desmatophocinae or the Allodesminae, and it has few diagnostic characters of either.

The P^4 and M^1 morphologies of *P. goedertae* are apparently substantially different from those of *Enaliarctos mealsi*. In the latter species, the P^4 was still a relatively fissiped-like carnassial tooth, but, based on the root morphologies, in *P. goedertae* it was apparently shaped more like the adjacent P^3 . The M^1 of *P. goedertae* has two roots more equal in size and aligned anteroposteriorly, and the cheek tooth row was thus more homodont. Following the use of the retained carnassial structure of the P^4 in defining the genera *Enaliarctos* and *Pinnarctidion*, and the subfamily Enaliarctinae (Mitchell and Tedford, 1973; Repenning and Tedford, 1977; Barnes, 1979), *Pteronarctos* belongs in the subfamily Enaliarctinae because it still has a carnassial, not yet having acquired a fully homodont cheek dentition. Also, its skull differs from those of the two species of *Enaliarctos* principally not by the presence or absence of diagnostic characters, but only in subtle proportional differences. Within the *Enaliarctos*–*Pteronarctos* group, it would be appropriate to draw the upper morphological limits of the subfamily at the first appearance of taxa that are demonstrated to have had homodont cheek teeth.

My previous interpretations (Barnes, 1979) of the phyletic position of *Pinnarctidion bishopi* remain unchanged. It shares many primitive characters and some derived characters with *Enaliarctos* spp. and *Pteronarctos goedertae*, but it has some other derived characters (e.g. ventrally placed optic foramen, broad palate, large paroccipital process, large orbit, dorso-ventrally expanded zygomatic process of the squamosal), which it shares with species of Allodesminae.

SUBFAMILY OTARIINAE

The subfamily Otariinae, which I use in the broad sense to include both fur seals (Arctocephalinae of some authors) and sea lions (e.g., Mitchell, 1968; Barnes, 1979), is here classified immediately following the Enaliarctinae to indicate its prim-

itive characters and the probable ancestral-descendant relationships between the two subfamilies. Within the Otariinae, I list the fur seals first, because they are the most primitive (King, 1983a:132; Morejohn, 1975; Repenning et al., 1971). *Pithanotaria starri*, of Late Miocene age, is the earliest known true otariine and, like the later types, had nearly homodont and double-rooted cheek teeth (P^1 is always single-rooted), but had lost the M^2 (a unique, derived character; see Repenning and Tedford, 1977:58–60, fig. 6). Among the species of *Arctocephalus*, *A. pusillus* is frequently regarded and the most like the sea lions (King, 1983a:37). *Zalophus californianus* (Lesson, 1828), the California sea lion, shares many characters with fur seals of the genus *Arctocephalus* (e.g., Kim et al., 1975; Morejohn, 1975; King, 1983a:16, 186) and, in fact, some limb bones of species in these two genera are almost indistinguishable. Van Gelder (1977), citing hybridization between the two genera (see also Mitchell, 1968; King, 1983a:186), synonymized *Zalophus* Gill, 1866, with *Arctocephalus*. I would not adopt such an extreme course, because the species of *Arctocephalus* form a cohesive generic unit (Repenning et al., 1971; Bonner, 1981; King, 1983a), but hybridization certainly reinforces ideas about the close relationship between the two genera, and this is partly the basis for not recognizing a separate subfamily, the Arctocephalinae, for fur seals (Mitchell, 1968; Repenning, 1976; Repenning and Tedford, 1977). (De Muizon [1978:182–183] recognized not only the subfamilies Otariinae and Arctocephalinae but yet another (new) subfamily, the Callorhinae, as well.) I have arranged the other sea lions in the Otariinae approximately in the order of increasing number of their derived cranial characters, with *Eumetopias* as the most derived (see Kim et al., 1975; Morejohn, 1975; King 1983a:16).

OTHER MIOCENE OTARIIDS

Early and Middle Miocene species of *Desmatophoca* were relatively highly derived, and the subfamily probably had a considerable earlier evolutionary history (see Barnes, 1987). Middle Miocene species of *Allodesmus* were, for their time, even more highly derived (Mitchell, 1966, 1968; Barnes, 1972; Repenning and Tedford, 1977) and had characters of the limbs that were convergent with those of Recent otariines. I have (Barnes, 1987) given arguments for maintaining these groups separate rather than linking them as was done by Repenning and Tedford (1977). The more slowly evolving subfamily Imagotariinae seems to have had a somewhat enaliarctine-like early member in *Neotherium mirum*, and the later lineages of the group rapidly increased in size and had evolved a nearly sea lion-like habitus by Late Miocene time (Repenning and Tedford, 1977). I have now reinterpreted the Late Miocene animal I called “Desmatophocine A” (Barnes, 1972) as an imagotariine near *Imagotaria* (see also Mitchell, 1975:21, fig. 1). Latest Miocene *Dusignathus santacruzensis* Kellogg, 1927, has a mandible with some characters that are shared in common with those of *Imagotaria* and other characters that are convergent with those of the primitive walrus *Prorosmarus allenii* Berry and Gregory, 1906 (Barnes, 1972; Mitchell, 1975), but its lower canines are

uniquely slender and elongate and its large, smooth-crowned cheek teeth are unlike those of *Imagotaria downsi*. Repenning and Tedford (1977) classified *Dusignathus* in the same subfamily as *Imagotaria* (thus placing the subfamily Imagotariinae in synonymy with the Dusignathinae), but I follow Mitchell (1968, 1975) in recognizing the separate subfamily Dusignathinae. The walruses (subfamily Odobeninae) appear to have been one of the last major groups of the Otariidae to have become differentiated, possibly in the latest Miocene and from the Imagotariinae (see Repenning and Tedford, 1977). Living walruses have remained relatively primitive postcranially while developing unusual cranial modifications that are correlated with tusk development. In recognition of similarities noted by Repenning and Tedford (1977), I classify *Valenictus* and *Pliopedia* in the Dusignathinae.

Fortunately, most of the recently named fossil species of Otariidae have been established on specimens that include at least the major part of a mandible or cranium. This is laudable taxonomic practice but has not always been the case, and the designation of disparate, noncomparable skeletal elements as holotypes has in some situations hindered subsequent objective comparisons. For example, *Pliopedia pacifica* Kellogg, 1921, *Neotherium mirum* Kellogg, 1931, and *Valenictus imperialensis* Mitchell, 1961, were each named on a few limb elements, or only one (in some instances noncomparable), and only later were other specimens assigned to these species. One of the first fossil otariids to be named, *Allodesmus kernensis* Kellogg, 1922, was originally based on a lower jaw, but the species is now known by skeletons with skulls from the same rock unit, the Round Mountain Silt, and is now the most completely known fossil otariid. The same deposit contains at least three other distinct taxa, one of which, *Pelagiartcos thomasi* Barnes, 1988, was recently named. Two that I had previously called desmatophocines I now place in the Allodesminae (see Mitchell, 1975).

Following are my comments on the fossil otariid species that have been named since Repenning and Tedford (1977) last reviewed the group. These taxa are arranged in the same sequence as they appear in the following classification.

CALLORHINUS GILMOREI BERTA AND DEMÉRÉ, 1986

A partial mandible, some teeth, and some postcranial bones from the San Diego Formation in southern California were used to describe this new taxon. It is Late Pliocene in age, from late Blancan correlative rocks exposed near San Diego.

The fossils are not complete but do indicate a small fur seal. This is the only Pliocene fossil fur seal species that has been named in the Pacific realm and the only nominal fossil pinniped from this time period.

ARCTOCEPHALUS (HYDRARCTOS) LOMASIENSIS DE MUIZON, 1978

This large species is the only named pre-Pleistocene southern hemisphere otariid. Its primitive cranial characters include the wide palate with posteriorly diverging cheek tooth rows and small supraorbital processes. Derived cranial characters

include the short, broad nasal bones; round root of I³; conical-crowned cheek teeth; and moderately advanced stage of cheek tooth root fusion (P¹⁻³ are single rooted, P⁴ and M¹⁻² have bilobed roots).

Dentally, this species is more derived than the earlier North Pacific fossil species of the genus *Thalassoleon*, but it has some more primitive cranial characters. I tentatively agree with de Muizon that the species can be contained within the genus *Arctocephalus*. In the absence of wide usage of subgenera within other pinniped groups, however, it serves little purpose to recognize a separate subgenus (*Hydrarctos*) for *A. lomasiensis*. Berta and Deméré (1986) elevated *Hydrarctos* to generic rank.

De Muizon pointed out that many (derived) characters of *A. lomasiensis* are shared with the Recent sea lions, particularly with the South American sea lion, *Otaria byronia*. These include the deep dentary with an abruptly upturned posterior end, which is unlike the condition in any living species of *Arctocephalus*. De Muizon (1978:fig. 4) presented a phylogeny in which fossil *Thalasseoleon* and Recent *Callorhinus* are an early side branch from the lineage leading to *Pithanotaria*; *Arctocephalus* is derived from *Pithanotaria*, and possibly gave rise to the sea lions; and *A. lomasiensis* (identified on the illustration as *A. [Hydrarctos] lomasi*) is an evolutionary dead end branching from *Arctocephalus*. I suspect that de Muizon's phylogenetic conclusions may be too explicit based on the fossil evidence, but they are in conformance with the generally accepted hypothesis that *Arctocephalus* is the living otariid group that is the closest to the primitive otariid groups, and is near the ancestry of the relatively more derived living sea lions.

NEOPHOCA PALATINA KING, 1983b

This species is based upon an abraded fossil skull from New Zealand. Its age was stated to be Middle Pleistocene, representing the New Zealand Castlecliffian Stage, and is possibly between 250,000 and 450,000 years old. The occurrence is outside of the current range of its apparently closest living relative, the Australian sea lion, *Neophoca cinerea* (Péron, 1816).

King noted that *N. palatina* differs from the Recent species in several characters including: wider basioccipital, expanding posteriorly; shorter palate; smaller cheek teeth, as indicated by the sizes of the alveoli; and less rugose tympanic bullae. These characters are primitive within the Otariidae, and King noted several points of resemblance between *N. palatina* and the primitive, latest Miocene fossil otariine, *Thalassoleon mexicanus* from Baja California. The broad interorbital region of both the living and fossil species of *Neophoca* is a derived character of this genus, and the absence of an anterior extension of the frontal on each side between the maxilla and nasal bone is apparently a unique derived character of *N. palatina*. As in most generalized Carnivora, the anterior extension of the frontal is present as a primitive condition in Otariidae, occurring in enaliarctines and otariines (including *N. cinerea*), and the absence of the extension in *N. palatina* is convergent with the derived condition in odobenines and imagotariines.

EUMETOPIAS OJIYAENSIS
HORIKAWA, 1981

This pinniped was found in rocks of "Plio-Pleistocene" age in central Japan and is presumably approximately two million years old. Nominally it is a member of the subfamily Otariinae, and I have classified it here as a more primitive taxon than the Recent northern Steller sea lion, *Eumetopias jubatus*. The holotype (the only known specimen) consists of some isolated teeth and postcranial bones of one individual. Unfortunately, no skull bones are known. The illustrated bones are characteristically otariine, and the lower cheek tooth has small anterior and posterior accessory cusps and a bilobed root (Horikawa, 1981:fig. 8), and the tibia is strongly bowed (Horikawa, 1981:pl. 1, fig. 45) as in *Eumetopias jubatus*. The bones are approximately the size of comparable ones of females of the living *E. jubatus*.

Compared with *Eumetopias jubatus*, *E. ojiyaensis* is more derived by having the root of the I² relatively more bulbous; the distal end of the first metacarpal more expanded transversely; the patella more circular in outline viewed from the anterior and not prolonged apically; and the astragalus with a shorter, broader neck and a more uniformly curved distal articular facet for the navicular. In this last character, the fossil species is similar to the earlier otariine *Thalassoleon mexicanus* (Repenning and Tedford, 1977:pl. 23, figs. 1, 3).

Eumetopias ojiyaensis has characters that are more derived than the living *E. jubatus* and, presuming that the generic assignment of the fossil is correct, this would preclude consideration of the fossil as being an ancestor of the living species.

DESMATOPHOCA BRACHYCEPHALA
BARNES, 1987

An insight into previously unknown diversity and antiquity of the subfamily Desmatophocinae was gained by discovery of this taxon. It is from Early Miocene rocks of the Astoria Formation in Washington and geochronologically older than *Desmatophoca oregonensis* Condon, 1906, from Oregon. It is interesting, however, that *D. brachycephala* has more highly derived characters than the later *D. oregonensis*. Neither species could be ancestral to the other, but they could share an earlier common ancestry.

Desmatophoca brachycephala was a relatively large species with a broad, low cranium; widely flaring zygomatic arches; and large canines. It is apparently a rare species and only one specimen has been found.

PROTOTARIA PRIMIGENA
TAKEYAMA AND OZAWA, 1984

Takeyama and Ozawa (1984) named this new fossil genus and species from Japan, based on an excellently preserved skull that was found with some associated postcranial bones of Middle Miocene age. Their paper is of a preliminary nature, and only the skull was briefly described and modestly illustrated. The authors classified *P. primigena* in the family

Enaliarctidae and concluded (Takeyama and Ozawa, 1984: 38) that it "... could have been derived from *Enaliarctos* and evolved to *Thalassoleon*, forming the main stock of the Otariidae ..."

The morphology of the holotype skull of *Prototaria primigena* closely resembles that of the unpublished topotypic, referred specimens (Barnes, in preparation) of the primitive imagotariine otariid, *Neotherium mirum* Kellogg, 1931, from the Sharktooth Hill Bonebed (UCMP 82362, 82363, 86132 and LACM 52172, 98147). Characters shared by the two taxa are: 1) mastoid process ventrolaterally directed and joined by a well developed, arcuate crest to a small, broad, posteriorly directed paroccipital process; 2) external acoustic meatus wide, not compressed anteroposteriorly between the mastoid process and postglenoid process; 3) tympanic bulla relatively uninflated and located posterior to the postglenoid process and not extended anteriorly ventral to the median lacerate foramen, and which is markedly concave just posterior to the postglenoid process; 4) glenoid fossa deep and large, with large preglenoid and postglenoid processes; 5) moderately developed sagittal crest that is most prominent dorsal to the anterior part of the braincase, not the posterior part; 6) similar facial angle; 7) premaxillae forming a broad and rounded, but not prominent, shelf anterior to nares; 8) crowns of upper canines oriented nearly vertically relative to the palate; 9) P¹ with a large, round root; 10) P³ with a relatively large remnant of the medial (protocone) root fused to the posterior (metacone) root and with a large postero-medial protocone shelf; and 11) P⁴ with a relatively large remnant root above the protocone located slightly antero-medial to the posterior (metacone) root.

Based on the above comparisons, I suggest that *Prototaria primigena* may be a species of *Neotherium*, and in the classification here I tentatively show the genus *Prototaria* as a junior synonym, yielding the new provisional binomen, *Neotherium primigenum*. The relationships of the Japanese taxon are, therefore, apparently not as was stated by Takeyama and Ozawa (1984). They suggested that *N. primigenum* could have evolved from *Enaliarctos*. This idea is consistent with the earlier suggestions that have been made by Mitchell and Tedford (1973:279) and Repenning and Tedford (1977:55, fig. 6) about the ancestry of *Neotherium* and that the enaliarctines are close to the possible ancestry of all later otariids but is contradictory to some features of anatomy. For example, *N. primigenum* has three roots on M¹ (Takeyama and Ozawa, 1984:38), a more primitive condition than in any species of *Enaliarctos* (or than in *Pteronarctos goedertae*) in which the M¹ is two-rooted, the posterior root being only bilobed. Additional and more detailed comparisons must be made before determining the more precise relationships between *N. primigenum* and *N. mirum*.

If my assignment of the Japanese fossil to the genus *Neotherium* is correct, the Japanese fossil is one of the earliest species in the subfamily Imagotariinae. There is neither morphological nor phylogenetic evidence, therefore, to suggest that *N. primigenum* was involved in the ancestry of the Otariinae, as was suggested by Takeyama and Ozawa. Additional evidence for my assertion lies in the differences between *N. primigenum* and the most otariine-like species of enaliarct-

tine, *Pteronarcos goedertae*. *Pteronarcos goedertae* differs from *Neotherium primigenum* by having: 1) broader, more U-shaped internal narial opening; 2) smaller pterygoid process of maxilla ventral to orbit; 3) flatter palate with largest palatine foramina located farther anteriorly, between P^4 's rather than between M^{1-2} 's; 4) alveoli for cheek teeth smaller; 5) less prominent strut of pterygoid lateral to the alisphenoid canal; 6) occipital condyles more divergent dorsally; 7) tympanic bulla more inflated; 8) braincase lower-vaulted and less anteroposteriorly elongated; 9) wider paroccipital process; 10) smaller posterior lacerate foramen; 11) zygomatic arches straighter, less bowed laterally, more slender, and less arched dorsally; 12) ear region positioned farther anteriorly on basicranium; 13) mastoid process smaller, more laterally directed, and not so cubic in shape; 14) infraorbital foramen smaller; 15) greater facial angle; 16) postorbital constriction less tapered posteriorly; 17) rostrum less parallel-sided, but instead, more tapered anteriorly, and not so swollen antero-laterally to accommodate the canine roots; 18) canine crown more procumbent; 19) anterior rostral extremity more pointed; 20) media (protocone) portion of root of P^4 located more posteriorly; 21) M^1 with larger posterior root that is also aligned more directly posterior to the anterior root; 22) mastoid process positioned relatively farther anteriorly, and external acoustic meatus resultantly more compressed anteroposteriorly; 23) nasal bones shorter, more expanded anteriorly, with more concave anterior margins and extending farther posteriorly on skull relative to anterior margin of orbit; 24) frontal not extending as far anteriorly between nasal and maxilla; 25) lambdoidal crests projecting farther posteriorly over occipital shield; 26) sagittal crest lower and shaped differently; and by being 27) 50 percent smaller.

PELAGIARCTOS THOMASI BARNES, 1988

This large species is apparently a member of the subfamily Imagotariinae, based on the morphology of the horizontal ramus of the dentary, on the outline of the symphyseal area, and on the cusp pattern of the cheek tooth crowns. I speculated (Barnes, 1988) that the animal may have been a predator on marine vertebrates. It is a rare animal, known only by a very few specimens from the Middle Miocene Sharktooth Hill Bonebed in California. It is distinguished by its large canines, whose roots are bilobed in cross section; its bulbous cheek tooth crowns; and its firmly ankylosed mandibular symphysis. This latter feature is convergent with unrelated extant walruses.

KAMTSCHATARCTOS SINELNIKOVAE DUBROVO, 1981

This species was described as the sole member of a new subfamily, the Kamtschatarctinae, which Dubrovo classified in the family Enaliarctidae. Her naming of this new subfamily only serves to further underscore my statements above about the unserviceability of an expanding otarioid classification that has an excess of family-group taxa with few included genera and species. Quite aside from that problem, however,

I suggest that there is little about the anatomy of *Kamtschatarctos sinelnikovae* to indicate that the species is an enaliarctine (or enaliarctid) in the sense in which it was defined by earlier writers. The holotype consists of a very incompletely preserved skull and a right dentary with four cheek teeth. The large skull is almost 50 percent larger than those of species of enaliarctinae, and it has wide glenoid fossae and a long, flat palate that are unlike those of any enaliarctines. The P^4 and M^{1-2} are each three-rooted, features that Dubrovo (1981, 1984) emphasized in distinguishing the new subfamily Kamtschatarctinae. The retention of three separate roots on each of these last three upper cheek teeth is a primitive character, however, and does not necessarily serve to diagnose the Kamtschatarctinae or to include *Kamtschatarctos* in the Enaliarctidae (= Enaliarctinae). The Early Miocene species of *Enaliarctos* actually represent a more derived state of cheek tooth root structure, with three roots present, as in *Kamtschatarctos sinelnikovae*, only on P^4 , two roots, rather than three, on M^1 (the posterior one being comprised of two coalesced roots), and only a single, bilobed root on M^2 (formed from two, or ultimately of three, coalesced roots, but never three separate roots).

Imagotaria downsi, which, depending on the classification one accepts, is either in a separate subfamily (either Imagotariinae or Dusignathinae) or family than Dubrovo has indicated for *Kamtschatarctos*, and has an upper cheek tooth root pattern that is similar to that of *Kamtschatarctos*, with two roots each on P^4 and M^1 , and in each, the posterior one being clearly bilobed and obviously formed from two coalesced roots, and three roots on M^2 (Repenning and Tedford, 1977:pl. 8, fig. 1). The pattern of the roots of P^4 - M^2 of *Imagotaria downsi* could have evolved simply through root coalescence from that of *Kamtschatarctos sinelnikovae*, but neither of these species could have evolved their root patterns from the more derived conditions that exist in any of the presently known species of Enaliarctinae.

Dubrovo (1984) further characterized *K. sinelnikovae* (and the subfamily Kamtschatarctinae) as lacking the P_1 . This is not the tooth that is usually lost in pinnipeds that have experienced cheek tooth reduction; it is the molars that are lost. I suggest that the loss of P_1 in the holotype of *K. sinelnikovae* is probably a nondiagnostic feature and more likely was the result of injury, pathology, or individual variability. Such random losses of teeth in otariids have been reported in fossil *Allodesmus kernensis* (Barnes, 1970:17, fig. 18, 1972:27, fig. 16), *A. packardi* (Barnes, 1972:49, fig. 19), *Imagotaria downsi* (Barnes, 1971:3, 6, figs. 1-3), in living *Zalophus californianus* (Barnes, 1970:20), *Callorhinus ursinus* (Scheffer and Kraus, 1964:312), and other Recent species of Otariinae (Mitchell, 1968:1847).

The dentary of *K. sinelnikovae* has a nearly straight ventral border and a small angular process. The mandibular condyle is positioned relatively low on the dentary, only slightly higher than the level of the cheek tooth row, and the coronoid process has a long, gently sloping anterior side and a nearly vertical posterior side that stops anterior to, rather than overhanging, the condyle. In these characters, the morphology of the dentary is most similar to mandibles that have been

referred to the imagotariine *Imagotaria downsi* (Barnes, 1971; Repenning and Tedford, 1977:22–23, pl. 5, figs. 2a, b). The closest relationships of *K. sinelnikovae*, therefore, seem not to be with enaliarctines, but rather with *Imagotaria*, and I classify *Kamtschatarctos* in the subfamily Imagotariinae and place the subfamily Kamtschatarctinae in synonymy. The available specimens and data indicate that within the Imagotariinae, *K. sinelnikovae* is more primitive than *Imagotaria downsi*, but further comparisons must be made between these and other species in the subfamily to verify the relationships that I have suggested.

The classification below includes all currently recognized fossil and living otariid species. I follow King (1978) and Oliva (1988) and recognize *Otaria byronia* as the valid species for the living South American sea lion. A “+” indicates a fossil taxon. Authors and dates within parentheses indicate a name that is used in a different context or rank than originally proposed.

Family Otariidae Gill, 1866

+Subfamily Enaliarctinae Mitchell and Tedford, 1973

- +*Enaliarctos* Mitchell and Tedford, 1973
- +*Enaliarctos mealsi* Mitchell and Tedford, 1973
- +*Enaliarctos mitchelli* Barnes, 1979
- +*Pteronarctos*, NEW GENUS
- +*Pteronarctos goedertae*, NEW SPECIES
- +*Pinnarctidion* Barnes, 1979
- +*Pinnarctidion bishopi* Barnes, 1979

Subfamily Otariinae (Gill, 1866) (incl. Arctocephalinae von Boetticher, 1934; Callorhinae de Muizon, 1978)

- +*Pithanotaria* Kellogg, 1925
- +*Pithanotaria starri* Kellogg, 1925
- Callorhinus* Gray, 1859
- +*Callorhinus gilmorei* Berta and Deméré, 1986
- Callorhinus ursinus* (Linnaeus, 1758)
- +*Thalassoleon* Repenning and Tedford, 1977
- +*Thalassoleon mexicanus* Repenning and Tedford, 1977
- +*Thalassoleon macnallyae* Repenning and Tedford, 1977
- Arctocephalus* Geoffroy Saint-Hilaire and Cuvier, 1826
- Arctocephalus philippii* (Peters, 1866)
- Arctocephalus townsendi* Merriam, 1897
- Arctocephalus galapagoensis* Heller, 1904
- Arctocephalus forsteri* (Lesson, 1828)
- Arctocephalus gazella* (Peters, 1875)
- Arctocephalus tropicalis* (Gray, 1872)
- +*Arctocephalus lomasiensis* de Muizon, 1978
- Arctocephalus australis* (Zimmerman, 1783)
- Arctocephalus pusillus* (Schreber, 1776)
- Zalophus* Gill, 1866
- Zalophus californianus* (Lesson, 1828)
- Phocarcos* Peters, 1866
- Phocarcos hookeri* (Gray, 1844)
- Neophoca* Gray, 1866
- +*Neophoca palatina* King, 1983b
- Neophoca cinerea* (Péron, 1816)
- Otaria* Péron, 1816

Otaria byronia (Blainville, 1820) (= *O. flavescens* [Shaw, 1800])

Eumetopias Gill, 1866

+*Eumetopias ojiyaensis* Horikawa, 1981

Eumetopias jubatus (Schreber, 1776)

+Subfamily Desmatophocinae (Hay, 1930)

- +*Desmatophoca* Condon, 1906
- +*Desmatophoca oregonensis* Condon, 1906
- +*Desmatophoca brachycephala* Barnes, 1987

+Subfamily Allodesminae (Kellogg, 1931)

- +*Allodesmus* Kellogg, 1922 (incl. *Atopotarus* Downs, 1956)
- +*Allodesmus courseni* (Downs, 1956)
- +*Allodesmus kernensis* Kellogg, 1922 (incl. *A. kelloggi* Mitchell, 1966)
- +*Allodesmus packardi* Barnes, 1972
- +“Desmatophocine B” of Barnes, 1972
- +“Desmatophocine C” of Barnes, 1972

+Subfamily Imagotariinae Mitchell, 1968 (incl. Kamtschatarctinae Dubrovo, 1981)

- +*Neotherium* Kellogg, 1931 (provisionally incl. *Prototaria* Takeyama and Ozawa, 1984)
- +*Neotherium primigenum* (Takeyama and Ozawa, 1984), PROVISIONAL NEW COMBINATION
- +*Neotherium mirum* Kellogg, 1931
- +*Pelagiarcos* Barnes, 1988
- +*Pelagiarcos thomasi* Barnes, 1988
- +*Kamtschatarctos* Dubrovo, 1981, NEW CONTEXT
- +*Kamtschatarctos sinelnikovae* Dubrovo, 1981
- +*Imagotaria* Mitchell, 1968
- +*Imagotaria downsi* Mitchell, 1968
- +“Desmatophocine A” of Barnes, 1972
- +*Pontolis* True, 1905
- +*Pontolis magnus* (True, 1905)

+Subfamily Dusingathinae Mitchell, 1968

- +*Dusingathus* Kellogg, 1927
- +*Dusingathus santacruzensis* Kellogg, 1927
- +*Pliopedia* Kellogg, 1921
- +*Pliopedia pacifica* Kellogg, 1921
- +*Valenictus* Mitchell, 1961
- +*Valenictus imperialensis* Mitchell, 1961

Subfamily Odobeninae (Allen, 1880)

- +*Aivukus* Repenning and Tedford, 1977
- +*Aivukus cedrosensis* Repenning and Tedford, 1977
- +*Prorosmarus* Berry and Gregory, 1906
- +*Prorosmarus alleni* Berry and Gregory, 1906
- +*Alachtherium* du Bus, 1867
- +*Alachtherium cretsii* du Bus, 1967
- +*Alachtherium antverpiensis* (Rutten, 1907)
- +*Trichecodon* Lankester, 1865
- +*Trichecodon huxleyi* Lankester, 1865
- +*Trichecodon koninckii* Van Beneden, 1877
- Odobenus* Brisson, 1762 (incl. ?*Hemicaulodon* Cope, 1869)
- Odobenus rosmarus* (Linnaeus, 1758)

Otariidae, incertae sedis

- +*Oriensarctos* Mitchell, 1968
- +*Oriensarctos watasei* (Matsumoto, 1925)

CONCLUSIONS

Pteronarctos goedertae, new genus and species, is the geochronologically youngest known taxon in the primitive otariid subfamily Enaliarctinae Mitchell and Tedford, 1973. The only known specimen of *P. goedertae* was collected from the base of the Astoria Formation (15 to 19 m.y.a.) near Newport, Oregon, and is late Early Miocene in age. The lower part of the Astoria Formation represents the lower part of the Newportian Molluscan Stage and is correlative with the Hemingfordian North American Land Mammal Age and the Burdigalian Stage of Europe, and the age of *P. goedertae* is, therefore, probably close to 19 million years. This is approximately 5 million years younger than the three previously described species of enaliarctines *Enaliarctos mealsi* Mitchell and Tedford, 1973, *E. mitchelli* Barnes, 1979, and *Pinnarctidion bishopi* Barnes, 1979, all of which are known from the early Early Miocene age Pyramid Hill Sand Member of the Jewett Sand in California. *Pteronarctos goedertae* is closely related to *Enaliarctos* and retains some primitive characters that exclude it from consideration as a descendant of either of the earlier species in that genus, but the two genera may have shared a common ancestry in Late Oligocene time. *Pteronarctos goedertae* shares certain derived characters with the living, relatively primitive species of fur seals in the genus *Arctocephalus* Geoffroy Saint-Hilaire and Cuvier, 1826, and is, therefore, within the otariid subfamily Enaliarctinae, the taxon that is closest to the ancestry of the modern subfamily Otariinae (sea lions and fur seals). The stage of evolution of *P. goedertae* suggests that the evolutionary transition from Enaliarctinae to Otariinae, although not yet demonstrated by fossils, occurred in the Middle Miocene. The cheek dentition of *P. goedertae* had evolved progressively somewhat in the direction of homodonty (such as exists in various derived otariids), but it retained a vestige of the carnassial structure characteristic of the earlier enaliarctines.

There is abundant evidence at present to suggest that otarioid pinnipeds are monophyletic. This, coupled with the fact that the various subfamilies Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, Dusignathinae, and Odobeninae share a suite of derived characters and that there are other characters shared among the subfamilies in various combinations, justifies their classification in a single family, the Otariidae, *sensu lato*. This family is comparable in morphologic and taxonomic diversity and in phylogenetic unity with some other families of mammals, including the true seals, the Phocidae.

A revised classification of the Otariidae includes seven subfamilies. It reflects mainly differences in rank rather than in implied relationships compared with the classification that was used by Repenning and Tedford (1977), which was designed to conform to the usage of suprageneric groups by neontologists. Systematic treatments of Recent taxa are changing, however, under the influence of data from the fossil record (compare Hall, 1981, *versus* Hall and Kelson, 1959). I propose the suppression of *Hydrarctos* de Muizon, 1978, as a subgenus of *Arctocephalus*, suppression of Callorhinae de Muizon, 1978, as a subfamily of Otariidae, provisional

synonymy of *Prototaria* Takeyama and Ozawa, 1984, with *Neotherium* Kellogg, 1931, provisional reassignment of the resulting *N. primigenum* (Takeyama and Ozawa, 1984), new combination, to the subfamily Imagotariinae, suppression of the subfamily Kamtschatarctinae Dubrovo, 1981, and inclusion of its type genus, *Kamtschatarctos* Dubrovo, 1981, in the subfamily Imagotariinae.

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